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Aspects of Social Organization and Diurnal Activity Patterns of California Bighorn Sheep

by R. Eccles

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ASPECTS OF SOCIAL ORGANIZATION AND DIURNAL ACTIVITY PATTERNS OF CALIFORNIA BIGHORN SHEEP (*Ovis canadensis californiana* Douglas 1829)

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October 1983

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INTRODUCTION

Ungulates have received considerable attention from ethologists and ecologists largely because of their often obvious and spectacular social nature (Geist 1971; Estes 1967, 1974; Jarman 1974; Kitchen 1974; Sinclair 1974). While some ungulates such as the moose (Alces alces) and chevrotain (Chevrotain tragulus) are solitary in nature, generally associating with conspecifics only during maternal and reproductive activities, the majority of species demonstrate a strong tendency for herding. Frequently, a hierarchial system has evolved to enable conspecifics to coexist in social units with a minimum of hostile interactions between group members. Social behaviour studies have shown that relatively linear dominance orders exist for some species such as cattle (Bos taurus) (Syme and Syme 1979), reindeer (Rangifer tarandus) (Espmark 1964), mountain sheep (Ovis canadensis, O. dalli) (Geist 1971) and that dominant status is positively correlated to body size, antler/horn size, and age. However, such studies have concentrated on male societies and their reproductive activities. This preoccupation with male behaviour is not surprising, considering the often spectacular nature of male interactions, but it has largely ignored the significance of the infrastructure of female-nursery groups. Since the social and behavioural development of animals of both sexes occurs in the company of adult females, the female society, by modifying the responses of young animals to environmental stimuli, is of fundamental importance to population stability and productivity. Some researchers have provided limited information on the social behaviour of ungulate nursery groups (Hafez 1969; Miller 1974; Kitchen 1974; Arnold and Dudzinski 1978), but more research is needed in this area to complete the socio-biological picture of many other ungulate species.

The concept of dominance in hierarchial systems also requires further consideration. While it has been suggested that occupants of rigidly defended territories have definite reproductive, foraging, and/or survival advantages over transient individuals (Wilson 1975), less reference has been made to the ecological benefits of dominant status in free ranging groups of animals. Wilson (1975) summarizes that "with rare exceptions, the aggressively superior animal displaces the subordinate from food, from mates and from nest sites." However, this statement is based largely on information from studies which have again concentrated on aspects of male interactions (Geist 1971). That high social rank in female hierarchies actually improves an individual's genetic fitness is more speculative and few studies have investigated this hypothesis.

The first objectives of this study were to investigate the social organization, and the apparent consequences of dominance in a captive group of adult California bighorn ewes. Hypotheses formulated and tested in the investigation in their alternative "H_A" form included:

Social Organization

1. A relatively stable linear hierarchy would be established amongst the ewes.

2. Age, horn size, and body size would be directly correlated to social status.

Consequences of Dominance

1. Dominant animals would, during months of limited available forage, have access to higher quality foraging areas and would, as a result, remain on a higher plane of nutrition than subordinate animals.

2. Access to high quality foraging areas would increase intake and assimilation rates and reduce the daily grazing times of dominants over those subordinates.

3. Dominant ewes, because of their higher plane of nutrition, would better survive the physiological stresses of winter and, as a result, would be in better physical condition and have a higher reproductive output than ewes of lower social rank.

The need for comparable data on the grazing times of individual herd members prompted an investigation into seasonal changes in the daily activity budgets of these animals as a second major research objective. For several decades, researchers of domestic animals have conducted such studies to determine the effects of environmental and physiological variables on the feeding behaviour and productivity of free ranging livestock (Meyer et al. 1957; Arnold 1960a, 1960b, 1962; Squires 1974; Arnold and Dudzinski 1978). Studies on domestic sheep (Ovis aries), for example, have shown that herd grazing times generally increase with seasonal declines in range quality and quantity (Arnold 1960a). Conversely, the degree of herd cohesion in free-ranging grazing animals often decreases with declining range conditions (Dudzinski and Arnold 1967; Dudzinski et al. 1969). Animal scientists have also reported that great daily variation in behaviour exists between individual herd members subjected to the same environmental conditions because of differences in age, sex, physiological condition, genetics, weight, and forage selection. Such information on herd and individual behaviour has, in turn, been employed in intensive range and animal management.

Similar studies on many wild ungulates are difficult because of the poor viewing conditions afforded by the animals' natural habitat. Few quantative data are available on the daily activity patterns and potential energy expenditures of mountain sheep for this reason. Various researchers (Mills 1937; Davis 1938; Blood 1963; Geist 1971) have described herd activity from relatively few days of observations, giving

the time of occurrence and duration of active and non-active periods for several different herds. Van Dyke (1978) completed a more thorough study of this kind, examining the activity patterns of ewes, lambs, and rams, and comparing the activity budgets of the different sex and age groups within seasons. However, researchers of wild populations are usually forced to observe different animals on different days and even fluctuating numbers on the same day. This obscures individual animal behaviour, resulting in "average data" being collected even for specific age and sex classes of animals. To understand fully and assess the activity budgets and potential energy expenditures of herd members, identifiable individuals must remain under observation throughout the study to interpret their daily behaviour with respect to the environmental and physiological factors mentioned above. The captive state and accessibility of the animals in this study provided such research opportunities. As a result, the secondary research objectives of this study were:

to determine the effects of range condition and season on the diurnal patterns and the activity budgets of a captive population of California bighorn sheep;

to assess the effects of physiological condition on the daily activity budgets of herd members;

to estimate the relative mean daily energy expenditures of the adult herd members on a monthly basis.

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STUDY AREA

In April 1977, a 40 ha enclosure adjacent to the Okanagan Game Farm, Penticton, B. C., was constructed for intensive studies on California bighorn sheep, a species native to the area. The enclosure, situated on steeply sloping grassland, falls within the Ponderosa Pine-Bunchgrass biogeoclimatic zone (Krajina and Brooke 1969) and is similar in both elevation and vegetation to the rangeland occupied year round by maternal groups of the Vaseux Lake bighorn population. However, the study area has a predominantly eastern aspect, differing from the Vaseux range which faces primarily west-southwest.

Before this study commenced, the enclosure had received only light, intermittent grazing from horses and was considered to be in a near climax successional stage (Wikeem, pers. comm.), being dominated by bluebunch wheatgrass (Agropyron spicatum). Estimates of the carrying capacity of the study site (Pitt, Wikeem, pers. comm.) dictated the size of the herd which was released into the area.

METHODS

FIELD PROCEDURES

From January to March, 1977, a drop net was used at the Vaseux Lake California bighorn range, 20 km south of Penticton, to capture animals for research at the study site. A total of 16 ewes, three lambs, and one yearling male was captured and transported to the Game Farm. Before being released into the enclosure in April, each animal was fitted with an identity collar.

Behavioural observations for this study commenced in May, 1977 and continued for 14 consecutive months. Most observations were made through a 20-40 x 60 zoom binocular spotting scope from a point 200 m east of the lower boundary of the enclosure where the majority of the study site could be viewed. This eliminated any obvious disturbance to the animals during sampling periods. When the animals occupied the northwestern corner of the enclosure, observations were made from a lightly timbered area approximately 50 m north of this portion of the study site.

Although water and mineral blocks were provided artificially in the northeast corner of the enclosure, the sheep were dependent for food on the bluebunch wheatgrass-big sage (Artemisia tridentata) plant community within the enclosure. As a result, their daily activity patterns were considered representative of free ranging animals on botanically similar ranges, particularly those populations not exhibiting seasonal, vertical migrations. In late December and throughout January, crusted snow conditions made foraging difficult for the sheep and several mortalities prompted the distribution of supplemental hay near the water and mineral supply. Approximately 45 kg of hay was provided at dusk each day. Behavioural data collected during this period were interpreted with

due consideration for the artificial feeding situation.

COMPARATIVE ANALYSIS - METHODS AND RATIONALE

Social Organization

1. Dominance hierarchy in the herd

To determine the social relationships existing between the captive ewes, observations of dyadic interactions were collected primarily by ad libitum sampling (Altmann 1974). Two assumptions necessary for such a sampling scheme to yield unbiased data, and considered fulfilled during the study were, a) that all behavioural patterns used in dominance interactions had an equal likelihood of being observed and, b) that the interactions of ewes of each social class had equal likelihood of being observed. Observations of interactions from ad libitum sampling were supplemented by those collected incidentally during scan sampling periods, a sampling method discussed in a later section.

Information recorded for each interaction included the identities of the initiator and receiver, behaviour patterns used by both as described by Geist (1971) and Shackleton (1973), and the nature of the interaction. Interactions were classified into one of five categories: bedding, feeding, positional, playful, or unclassified (where interaction was already in progress, making classification impossible).

A "dominant" animal was defined as an individual which displaced a fellow herd member from a resource (i.e. bedding site, feeding site, etc.), or as an individual to which subordinate behaviour (Geist 1971) was directed. This information was tabulated in two interaction matrices each of "Dominants" and "Subordinates", the first containing data collected from May 1977 to December 1977; the second constructed from data gathered from February 1978 to June 1978 after the structure of the herd had been altered by mid-winter mortalities. The cells of each matrix contained the number and outcome of disputes occurring between every pair of herd members for that particular time period. Each animal was then ranked according to the number and identity of fellow herd members that it had dominated and had been dominated by. Neither the 18 lambs born on site in 1977 nor the three yearlings were included in these analyses since the majority of their interactions were play-like and difficult to interpret. A Dominance Value (D.V. = arcsin $\sqrt{x}$, where x = proportion of opponents dominated (Beilharz et al. 1966)) was determined for each animal from the proportion of opponents that it dominated. D.V.'s have been employed to rank individuals socially within a group of animals in situations where such a process is not possible from a quantitative analysis of dyadic encounters alone, either because of dominance circles or a lack of actual social interactions between certain pairs of animals. (Such a situation arose for the captive herd; see Results). Providing each herd member is involved in a sufficient and comparable number of interactions, a D.V. can be assigned to each animal, regardless of the identity of its opponents. In addition, these values, once converted by an arcsin transformation, become normally distributed, enabling parametric correlations between rank and biological parameters to be made. Several different methods of estimating D.V.'s have been

developed (angular D.V.'s, used in this study, weighted angular D.V.'s, least-square D.V.'s). However, Beilharz et al. (1966) found that ..."the three measures of social dominance gave practically identical evaluations of dominance." From analysis of the Dominance Values, three distinct social classes were recognized among the adult ewes. A description of these three groups labelled Dominants, Intermediates, and Subordinates, is given in the Results section.

Landau's index of linearity was also determined for each hierarchy, an index which provides a measure of the degree of linearity for any given hierarchy (Wilson 1975). In formula:

$$h = \frac{12}{n^3-n} \sum_{i=1}^{n} (V_i - (n-1)/2)^2$$

where h = Landau's index
n = the number of animals in the study group
V_i = the number of group members that the i^{th} animal dominates

Values range from 0 to 1, with 1 indicating a completely linear order.

2. Determinants of dominance

To determine if predicted morphological criteria were important in determining social rank in the adult ewes, ages (estimated by horn annuli (Geist 1966)), body weights, and horn lengths were collected from each animal four times during the course of the study (September and December, 1977; March and August, 1978). The degree of correlation between Dominance Values and age, mean weights, and horn lengths was determined for the herd members in each of the hierarchies.

To investigate the importance of behavioural as well as morphological parameters to dominance, the number of aggressive encounters initiated by each individual was tallied for both the 1977 and 1978 hierarchies. The degree of correlation between these totals and respective Dominance Values was then assessed.

A level of 5% probability was established *a priori* for this and all subsequent statistical analysis.

Consequences of Dominance

1. Diet comparisons

Two separate approaches were taken to compare diets of the three social classes of ewes. In January, 1978, the herd demonstrated an apparent "preference" for the supplemental hay over the more abundant range forage, depleting the hay supply before starting their grazing routine. Following a similar approach to that of Espmark's (1974a, 1974b) studies on roe deer (*Capreolus capreolus*) and reindeer, the mean daily time spent by each social class consuming hay was compared (method of data collection will be discussed in a later section). A

Student's t-test was used to test the hypothesis that dominant ewes would gain greater access to the "preferred" feed than intermediate or subordinate ewes.

Use of fecal nitrogen (N) levels was the second, more indirect, approach to diet comparisons. Hebert (1973) found fecal N levels to be positively correlated to crude protein and energy levels of forage consumed by bighorn sheep. Recognizing this fact, fecal samples were collected from ewes of different social status during recaptures in December, 1977 and March, 1978. Mean N Levels in feces of dominants were then compared to those of intermediate and subordinate ewes, again using Student's t-test.

2. Activity budget comparisons

Comparisons of the mean daily grazing and bedding times of the three social classes of ewes were conducted based on the findings of domestic animal studies. Arnold (1960a) showed that the grazing time of domestic sheep increased and ruminating time decreased with decreasing pasture quality. For this study, it was postulated that dominant ewes would, in general, forage on higher quality vegetation and, as a result, would demonstrate reduced feeding times and lowered energy expenditures than intermediate and subordinate ewes forced into more marginally nutritious areas.

Scan sampling (Altmann 1974) was used to collect data on the activity durations, movements, and locations of individual ewes for this comparative analysis. On three to eight sampling days per month, the study site was scanned every 15 minutes from dawn to dusk and individual activity and quadrat location (from a gridded photograph) was noted. Although each animal was observed for only five seconds, approximately two to ten minutes were required for a complete scan of the herd, depending on the degree of herd dispersion and movement. Activities were categorized as feeding, bedding, travelling without feeding, standing, and other (play, social interactions, grooming). The time devoted to these activities during the daylight hours was calculated each day for each animal. Only data collected on feeding and bedding times from September, 1977 to March, 1978 were utilized for this particular analysis, since it was assumed that high quality forage would be limited and that competition between conspecifics would be evident only during this period.

The variation in the mean daily feeding and bedding times of the different social classes of adult ewes was assessed each month by analysis of variance, using a two factor analysis with one interaction term and an unbalanced nested term. In linear model form:

$$Y_{ijk} = \mu + G_i + D_j + (GxD)ij + N_{K(i)} + [(GxD)ijxN_{K(i)}]$$

where Yijk = daylight time devoted to grazing (or bedding)
μ = herd mean

G_i = social group effect (three levels)
D_j = sampling day effect (three to eight levels, depending on month
$(GxD)ij$ = group x day interaction term
$N_{K(i)}$ = animal within social group effect (unbalanced nested term).
Levels of the nested terms decreased slightly as the study progressed because of mortalities and herd reduction.
$(GxD)ijxN_{K(i)}$ = experimental error term.

The LSM 76 computer program (Harvey 1977) was used for the analysis.

3. Productivity comparisons

Several production parameters were compared among ewes of different social status. Seasonal weight change was one such parameter. It was hypothesized that dominant animals, with access to high quality forage would maintain a more constant body weight than subordinate animals. To test this hypothesis, the average October to December, 1977 weight loss of dominant ewes was compared (t-tests) to that of each of the remaining two social classes. Similarly, mean weight gains between March and August, 1978 were also compared. In each case, weight changes were expressed as a proportion of the original weight (i.e. October and March weights).

Unexpected mortalities in the herd in December, 1977 allowed an a posteriori comparison of fitness between social groups. Using a Chi-square goodness of fit test, the observed frequencies of deaths from the three social classes were compared to expected values. Expected values were calculated from the total number of deaths and the proportion of animals in each social class.

Reproductive measures were used as a third comparison. Research on nutrition in domestic sheep has demonstrated the significance of pre-partum diet quality of dams on birthweight and survival of the neonate (Alexander 1961). Therefore, one may expect a dominant ewe, by maintaining a higher nutritional plane than subordinate animals, to be reproductively more successful than the latter.

In 1978, when only five of the ten potentially productive ewes produced lambs, the expected and observed frequencies of births from the three social classes were compared by a Chi-square goodnes of fit test. Expected frequencies were calculated from the total number of lambs produced and the number of ewes of each class comprising the herd. This was not possible for 1977, since every captive ewe produced at least one lamb. Birth weights of the lambs were not available for comparison.

Forage Availability and Herd Behaviour

Information on forage availability and selection by the sheep was available from the vegetation study occurring simultaneously with this

behavioural work (Pitt and Wikeem 1979; unpubl. data). Consequently, it was possible to consider the effect of range phenology and animal diet on the activity patterns and budgets of the herd.

1. Seasonal diurnal patterns

As previously described, scan sampling was used to collect information on the diurnal activity patterns of herd members. For every sampling day in a month, the proportion of the herd active (all activities other than bedding) at each 15 minute sampling interval throughout the daylight period was calculated. These values were, in turn, used to determine the mean daily number and distribution of activity peaks for every month of the year. More than 50% of the herd had to be active for at least two consecutive sampling intervals (i.e. 30 minutes) to constitute an activity peak. Similarly, a non-active period was recognized only if 50% or more of the herd remained bedded for at least two consecutive sampling intervals.

2. Seasonal activity budgets

The activity data collected during each 15 minute scan sampling interval enabled seasonal trends in the daily activity budgets of the herd members to be monitored. Estimates of total daylight times (in hours) devoted to foraging, bedding, travelling, standing, and "other" activities were determined each day by summing the number of 15 minute sampling intervals in which an activity was observed and dividing by four. Mean daily values were then calculated for each ewe and for the herd as a whole on a monthly basis.

Using a high intensity spot lamp and the spotting scope, the herd was monitored on four occasions (May 5, June 20, and November 14, 1977, and December 17, 1978) to determine the extent of night-time activity. However, individual animals could not be identified during such observations and night data were not included in monthly activity budget determinations.

Effects of Physiological Condition on Activity Budgets

Activity budget comparisons were conducted from October to April between animals of different physiological condition. Analysis of blood samples collected from the ewes in the September-October recapture program (Peterson, pers. comm.) showed elevated levels of SGOT, an enzyme indicative of body tissue catabolism, in six ewes. With one exception, all ewes demonstrating these high levels died during December or January. Grazing and bedding durations of these moribund animals in the three months prior to their death were compared to those of healthy animals within their respective social class by Student's t-test.

Feeding and bedding times of pregnant and non-pregnant ewes were compared in March and April, the two final months of pregnancy when fetal demands would be greatest. Similar to the fall comparisons, only data

from ewes of the same social class were compared to prevent factor confounding. Student's t-test was again used.

Energy Expenditure Estimates for the Herd

Using the bioenergetic literature available on mountain sheep (Chappel 1978), domestic sheep (Graham 1964; Clapperton 1961, cited in Moen 1973), the mean daily activity budgets of the herd were converted to mean daily energy expenditure estimates for each month. Chappel (1978) developed a predictive bioenergetic model for bighorn sheep which estimates fasting and resting metabolic rate (FMR and RMR, respectively), given the sex, weight, nutritional status (fed or fasted), gross energy intake of the animal, date of the trial, trial temperature, and mean ambient temperature three days prior to the trial. With the exception of gross energy intake values, which had a relatively low predictive value in the overall model, information on all of the above factors was available for this study. Monthly mean ewe weights were taken from interpolated points on a graph of weights obtained during five capture programs. Weather data from the Penticton airport, five km from the study site, provided the necessary temperatures. The mean temperature on sampling days was used as the trial temperature, while the monthly mean temperature was used as the ambient temperature.

To determine the daily energy expended by an animal on a given activity, various conversion factors have been developed which are generally applied to that animal's basal metabolic rate. Basal metabolism, defined as "the minimal energy cost when an animal is at rest in a thermoneutral environment and in a post absorptive condition" (Brody 1945, cited in Moen 1973), is a difficult condition to achieve in ruminants during metabolic research because of long retention times of food in the ruminant stomach and the tendency of study animals to stand rather than lie in metabolic chambers. As a result, FMR's measured from fasted animals (36 - 72 h) generally in a standing position, have been more recently used as an appropriate equivalent (Blaxter 1962). In this study, average daily FMR values minus the added costs of standing (based on Chappel's (1978) findings) were used as estimates of BMR values in the calculation of daily energy expenditures.

Energy conversion factors for activities were taken from various sources. The additional energy costs of both standing and feeding for ewes (0.22 kcal/kg/h and 0.43 kcal/kg/h, respectively) were taken from Chappel's (1978) work while ruminating increments (0.24 kcal/kg/h) applied to bedding times and running increments (8 x BMR kcal/kg/h) above BMR were taken from the research of Graham (1964) and Hammel (1962, cited in Moen 1973), respectively. Clapperton's estimate (1961, cited in Moen 1973) of walking costs (0.59 kcal/kg/km) was used in this study. It was assumed that all travelling was done along contours (an assumption fulfilled the majority of the time) and that the animals walked at the rate of 5 km/h. This negated the need for estimates of the distance travelled by the animals, values not confidently obtained from the data collected, and converted the energy costs of walking to kcal/kg/h. Costs of activities labelled "other" (interacting, playing) were estimated from Moen's (1973) conversion factor for play (3xBMR kcal/kg/h). Pregnancy and lactation

demands were also considered, using approximate energy expenditures presented in Moen (1973) for such levels of production. Moen estimated that a 60 kg deer's maintenance requirements (normal daily activity costs) are approximately 1.42 x BMR. This multiple increases to 1.52 (1.08 x activity costs) by the end of gestation and to 1.86 (1.31 x activity costs) during peak lactation with one fawn. The multiples in brackets were applied to daily energy expenditures in appropriate months (April for pregnancy, May for peak lactation) in this study.

The average total energy expended during the daylight hours was determined for each month and converted to an hourly rate of consumption. This value was then expressed as a multiple of the herd's mean FMR for that month. The proportion of energy expended on each activity during the day was also calculated each month.

The general calculation procedures for the energy expenditure estimates were as follows:

Grazing : $Q_{Gi} = [BMR_i + 0.43\ (Wt_i)]\ T_{Gi}$

Bedding-ruminating : $Q_{B/Ri} = [BMR_i + 0.24\ (Wt_i)]\ T_{B/Ri}$

Walking (5 km/h) : $Q_{Wi} = [BMR_i + 0.59\ (Wt_i)V]\ T_{Wi}$

Running : $Q_{Ri} = [BMR_i + 8.0\ (BMR_i)]\ T_{Ri}$

Standing : $Q_{Si} = [BMR_i + 0.22\ (Wt_i)]\ T_{Si}$

"Other" activities : $Q_{Oi} = [BMR_i + 3\ (BMR_i)]\ T_{Oi}$

where Q_{Gi}, $Q_{B/Ri}$, Q_{Wi}, Q_{Ri}, Q_{Si}, Q_{Oi} = average daylight energy expended on grazing, bedding/ruminating, walking, running, standing, and "other" activities, respectively, during the i^{th} month (kcal).

BMR_i = average daylight energy expended on basal metabolism during the i^{th} month (kcal/h).

Wt_i = average weight of adult ewes during the i^{th} month (kg).

V = velocity of travel (5 km/h).

T_{Gi}, $T_{B/Ri}$, T_{Wi}, T_{Ri}, T_{Si}, T_{Oi} = average daylight time devoted to grazing,[1] bedding/ruminating, walking,[2] running,[3] standing, and "other" activities, respectively, during the i^{th} month(h).

---

[1] Conversion factors for grazing, bedding/ruminating, and standing have units of kcal/kg/h.

[2] Conversion factor for walking has units of kcal/kg/km.

[3] Conversion factors for running and "other" activities are unitless.

RESULTS

SOCIAL ORGANIZATION

Dominance hierarchy in the herd

A total of 180 interactions between adult ewes were observed during the study. These interactions were typically sudden, brief encounters (< 10 sec). Ewes demonstrated a very limited behavioural repertoire, performing only two or three different patterns in the majority of interactions. Butting was the most common pattern used by dominants to displace subordinate animals, followed in frequency by the horn threat. The subordinate's response was usually to squat, urinate, and then move from the area, or simply to flee. However, mild clashes, followed by several seconds of horn wrestling in which interactors would lock horns and push or twist heads, often resulted from the initial butt, regardless of the difference in social rank of the interactors. Almost invariably (> 90%), the initiator of such an encounter was the eventual dominant. Other patterns used infrequently by dominant ewes towards subordinates included the low stretch and kick. Subordinate animals occasionally displayed head shakes or threat jumps after being displaced by dominants and, on two occasions, were observed nuzzling more dominant animals.

Of the five categories of interactions, encounters at bedding sites were those most frequently observed throughout the year, comprising 60 (33%) of the 180 interactions recorded. Fifty-one interactions (28% of the total) occurred at feeding sites, including the supplemental mineral, water, and feed sources. Positional interactions arose primarily when subordinate animals appeared to violate the "individual distance" (Syme and Syme 1979) of more dominant animals. Forty-six (26%) of all interactions classified were of this type. Playful interactions were considered to be those encounters not associated with resources or positioning. Play was characterized by erratic behaviour patterns (jumps, bursts of running, exaggerated horn threats) not normally observed in daily maintenance behaviour. Such interactions between adult ewes, usually initiated by the playful behaviour of yearlings and lambs, were most prevalent in the spring (late March to June), tapering off in frequency as the summer progressed and becoming rare to non-existent during the fall and winter. Because of this seasonal trend, playful interactions comprised only 7% (13) of all adult encounters for the entire year. The remaining 10 interactions (5%) were unclassified. Ritualized dominance disputes typical of bighorn rams (Geist 1971; Shackleton 1973) were not observed during the 14-month study.

As well as being brief, interactions between adult ewes were so infrequent that encounters between some pairs of animals were never observed. As a result, several cells of each interaction matrix (Tables 1 and 2) contain no information on the social relationships between particular pairs of ewes. However, computation of Dominance Values enabled a social rank to be assigned to each individual. An evaluation of the Dominance Values, in turn, showed the existence of three relatively distinct social groups for both time periods. For the June to December, 1977, sampling period (Table 1), four ewes (WWW, W, RWB, WW)

Table 1. Dominance Values of captive ewes, based on dyadic interactions, June 1 to December 31, 1977.

i		Animal Identification Codes															Xi Prop. of opponents dominated by i	Dominance Value = ARCSIN$\sqrt{Xi}$
		WWW	W	RWB	WW	BIBI	RB	BW	W/B	NCT	PBC	R/B	RBR	W/R	NCA	WBW		
1	WWW		[a]+(2)	(0)	(0)	(0)	(0)	+(1)	(0)	+(2)	+(2)	+(1)	+(1)	+(1)	+(1)	(0)	1.00	90.0
2	W	-(2)		+(3)	(0)	(0)	+(3)	+(1)	+(1)	(0)	+(1)	+(3)	-‡(4)	+(1)	+(1)	+(1)	0.89	70.3
3	RWB	(0)	-(3)		[b]±(2)	+(1)	+(1)	(0)	(0)	+(4)	(0)	(0)	+(1)	+(2)	+(1)	+(2)	0.83	65.9
4	WW	(0)	(0)	±(2)		-(1)	(0)	(0)	+(2)	+(1)	+(1)	+(1)	(0)	+(1)	+(3)	+(1)	0.83	65.9
5	BIBI	(0)	(0)	-(1)	+(1)		-(1)	+(1)	(0)	(0)	+(2)	+(1)	(0)	(0)	(0)	(0)	0.67	54.7
6	RB	(0)	-(3)	-(1)	(0)	+(1)		(0)	±(2)	(0)	±(2)	+(1)	+(2)	(0)	(0)	+(3)	0.63	52.2
7	BW	-(1)	-(1)	(0)	-(2)	-(1)	(0)		(0)	(0)	+(2)	(0)	(0)	(0)	+(1)	+(1)	0.50	45.0
8	W/B	(0)	-(1)	(0)	-(1)	(0)	±(2)	(0)		(0)	+(5)	(0)	+(2)	(0)	(0)	(0)	0.50	45.0
9	NCT	-(2)	(0)	-(4)	-(1)	(0)	(0)	(0)	(0)		(0)	-(1)	(0)	+(2)	+(2)	+(1)	0.43	40.9
10	PBC	-(2)	-(1)	(0)	-(1)	-(2)	±(2)	-(2)	-(5)	(0)		(0)	+(1)	+(1)	+(1)	+(3)	0.41	39.8
11	R/B	-(1)	-(3)	(0)	-(1)	-(1)	-(1)	(0)	(0)	+(1)	(0)		-(1)	+(1)	+(1)	+(2)	0.40	39.2
12	RBR	-(1)	∓(4)	-(1)	(0)	(0)	-(2)	(0)	-(2)	(0)	-(1)	+(1)		+(1)	+(2)	(0)	0.36	36.9
13	W/R	-(1)	-(1)	-(2)	-(1)	(0)	(0)	(0)	(0)	-(2)	-(1)	-(1)	-(1)		±(2)	+(2)	0.15	22.8
14	NCA	-(1)	-(1)	-(1)	-(3)	(0)	(0)	-(1)	(0)	-(2)	-(1)	-(1)	-(2)	±(2)		+(3)	0.14	21.7
15	WBW	(0)	-(1)	-(2)	-(1)	(0)	-(3)	-(1)	(0)	-(1)	-(3)	-(2)	(0)	-(2)	-(3)		0.00	0.0

Linearity of hierarchy, based on Landau's Index: 0.59

[a] When reading across Tables 1 and 2, plus signs indicate dominance, minus signs subordination. When reading down, reverse is true. The number of interactions between each pair of ewes is given in parentheses.

[b] Indicates dominance reversal in successive interactions.

Table 2. Dominance Values of captive ewes, based on dyadic interactions, January 1 to June 30, 1978.

i		Animal Identification Codes										Xi Prop. of opponents dominated by i	Dominance Value = ARCSIN$\sqrt{Xi}$
		R/B	W	WW	RWB	NCT	RB	RBR	W/R	NCA	WBW		
1	R/B		(0)	(0)	[a]+(1)	+(5)	+(1)	(0)	+(1)	+(1)	+(1)	1.00	90.0
2	W	(0)		[b]±(2)	+(3)	+(2)	+(4)	(0)	+(4)	(0)	(0)	0.90	71.6
3	WW	(0)	±(2)		-(4)	+(2)	+(1)	+(1)	+(5)	+(2)	(0)	0.79	62.4
4	RWB	-(1)	-(3)	+(4)		+(5)	+(2)	+(3)	+(1)	+(3)	+(2)	0.78	61.9
5	NCT	-(5)	-(2)	-(2)	-(5)		+(1)	+(2)	+(2)	+(1)	+(1)	0.56	48.2
6	RB	-(1)	-(4)	-(1)	-(2)	-(1)		+(2)	±(2)	+(1)	+(2)	0.39	38.6
7	RBR	(0)	(0)	-(1)	-(3)	-(2)	-(2)		(0)	+(1)	+(1)	0.33	35.3
8	W/R	-(1)	-(4)	-(5)	-(1)	-(2)	±(2)	(0)		(0)	+(3)	0.21	27.6
9	NCA	-(1)	(0)	-(2)	-(3)	-(1)	-(1)	-(1)	(0)		+(1)	0.14	22.2
10	WBW	-(1)	(0)	(0)	-(2)	-(1)	-(2)	-(1)	-(3)	-(1)		0.00	0.0

Linearity of hierarchy, based on Landau's Index: 0.46

[a] When reading across Tables 1 and 2, plus signs indicate dominance, minus signs subordination. When reading down, reverse is true. The number of interactions between each pair of ewes is given in parentheses.

[b] Indicates dominance reversal in successive interactions.

were dominant over much of the herd and had high Dominance Values, ranging from 65.9 to 90.0. Three ewes (WBW, NCA, W/R) were subordinate to the majority of herd members and had relatively small values (22.8 to 0.0). The remaining animals of intermediate status were dominant over and dominated by approximately the same number of animals. As a result, Dominance Values for these animals clustered around the mid-point of 45.0, ranging from 36.9 to 54.7. For the January to June, 1978 sampling period (Table 2), the three groups were again evident but of slightly different composition. Four dominant (R/B, W, WW, RWB) and three subordinate animals (W/R, NCA, WBW) were again clearly definable from their high (61.9 to 90.0) and low (27.6 to 0.0) Dominance Values, respectively. Intermediate animals (NCT, RB, RBR), greatly reduced in numbers because of winter mortalities, had values ranging from 35.3 to only 48.2.

It was hypothesized that a strongly linear hierarchy would develop within the captive herd. However, findings presented below forced the rejection of this hypothesis. Although the animals could be ranked linearly from their Dominance Values, the hierarchies showed poor linearity, based on Landau's index (0.59 and 0.46, respectively for the 1977 and 1978 hierarchies). A hierarchy with a score of 0.9 or greater is generally judged to be strongly linear (Wilson 1975). It would appear that the low index values largely resulted from the lack of interactions between many pairs of herd members and the abundance of dominance reversals. There were no established dominance circles evident in either hierarchy to contribute to their non-linearity.

Stability of the herd's social system

The analysis of herd interactions for two different time periods enabled the stability of the herd's social system to be evaluated over a one year period. Winter mortalities resulted in the loss of five adult ewes from the herd (one dominant - WWW; four intermediates - PBC, W/B, BLBL, BW). Although most animals retained relatively constant Dominance Values and social positions after this reduction, some rank changes were evident. R/B moved from a low intermediate status (D.V. = 39.1) to a very high ranking position (D.V. = 90.0), revealing her increased dominance first in late April, 1978 and then more conclusively in May and June. NCT made a more moderate climb, reversing positions with RB within the intermediate social class. Her increased dominance was first noted in mid-May, 1978. RB showed a considerable decrease in her Dominance Value, dropping from 52.2 in 1977 to 38.3 in 1978.

In July, 1977, a ewe from the Game Farm paddocks jumped into the study enclosure and joined the captive herd. This occurrence caused no apparent increase in the number of aggressive interactions within the herd nor did it disrupt the established hierarchy. The ewe appeared to be a relatively dominant animal, although her stay was too limited to assess her status accurately.

Determinants of dominance

The predicted determinants of dominance (age, horn length, body weight) were not clearly related to social status in the herd. Age estimates did demonstrate that the three most subordinate ewes in each hierarchy were the youngest adults (three years of age) in the herd. However, a four-year-old ewe was one of the four most dominant ewes in each hierarchy. Since age estimates by horn annuli were only considered accurate up to six years, ages could not be correlated to social rank for the majority of the ewes.

In 1977, weights and Dominance Values were poorly correlated ($r = 0.33$) but significantly correlated in 1978 ($r = 0.55$; $p < 0.05$) (Tables 3 and 4). The reverse was true for horn lengths, with the horn length - D.V. correlation coefficients in 1977 and 1978 being 0.61 ($p < 0.05$) and 0.35 (not sig.), respectively.

Although no morphological criteria were strongly correlated to dominance in both 1977 and 1978, aggressiveness appeared to be a consistently significant requirement for high social status. In both hierarchies, the number of aggressive interactions initiated by an individual showed a high, positive correlation to Dominance Value ($r_{1977} = 0.76$; $r_{1978} = 0.81$; $p < 0.05$). Alternatively, aggressiveness may have been a result, rather than a determinant of dominance, and dominance may have been attributed to some other, more subtle factor(s).

Based on these results, the hypothesis that age, horn length, and body weight were consistent determinants of social status had to be rejected.

CONSEQUENCES OF DOMINANCE

Diet comparisons

It was predicted that dominant animals would, during months of limited available forage, have greater access to high quality feeding sites and would remain on a higher plane of nutrition than more subordinate animals. However, results of the diet comparisons conducted between social groups forced the rejection of this hypothesis. Neither the times spent at high quality, supplemental feed in January (Table 5a), nor the fecal N levels found in December, 1977 and March, 1978 samples (Table 5b) were significantly different between social groups.

Activity budget comparisons

The hypothesis that dominant animals would show shorter grazing times and longer bedding times than more subordinate animals during potential months of shortages in high quality forage was also rejected. The grazing times of the three social classes did not differ in the months used for comparisons (September to March). Some differences did arise in bedding times, although not in the manner predicted. In October, the mean bedding time of Dominants was statistically similar

Table 3. Correlation between Dominance Values (D.V.) and predicted determinants of dominance: age, body weight, horn length and aggressiveness, June to December, 1977.

Social Class	Animal I.D.	D.V.	Age	Mean 1977 Weight (kg)	Mean 1977 Horn Length (mm)	Aggressiveness
Dominants	WWW	90.00	6+	50.5	302.5	9
	W	70.3	6+	50.5	275.0	15
	RWB	65.9	4	56.5	271.0	11
	WW	65.9	6+	60.5	277.5	8
Intermediates	BIBI	54.7	6+	46.5	280.0	3
	RB	52.2	6+	53.0	270.0	9
	BW	45.0	6+	52.5	280.0	3
	W/B	45.0	6+	50.0	305.0	6
	NCT	40.9	6+	50.5	264.5	4
	PBC	39.8	6+	49.5	230.0	6
	R/B	39.2	6+	55.0	262.0	4
	RBR	36.9	6+	56.5	287.5	4
Subordinates	W/R	22.8	3	52.0	244.5	2
	NCA	21.7	3	52.0	230.0	4
	WBW	0.0	3	44.5	253.0	0

Correlation coefficients: $r_{A.}$ not obtainable with aging techniques used

$r_{WT.} = 0.33$ (NS)

$r_{H.L.} = 0.61$ ($p < 0.05$)

$r_{AG.} = 0.79$ ($p < 0.05$)

Table 4. Correlation between Dominance Values (D.V.) and possible determinants of dominance, January to June, 1978.

Social Class	Animal I.D.	D.V.	Age	Mean 1978 Weight (kg)	Mean 1978 Horn Length (mm)	Aggressiveness
Dominants	R/B	90.00	6+	55.0	261.5	10
	W	71.6	6+	51.0	277.0	13
	WW	62.4	6+	55.0	280.5	12
	RWB	61.9	5	57.0	271.0	17
Intermediates	NCT	48.2	6+	51.0	269.5	7
	RB	38.6	6+	51.5	270.0	5
	RBR	35.3	6+	55.0	291.0	1
Subordinates	W/R	27.6	4	50.5	250.0	4
	NCA	22.2	4	52.5	233.0	0
	WBW	0.0	4	45.0	261.0	0

Correlation coefficients: $r_{A.}$ not obtainable with aging techniques used

$r_{WT.} = 0.67$ ($p < 0.05$)

$r_{H.L.} = 0.36$

$r_{AG.} = 0.81$ ($p < 0.05$)

Table 5. Diet comparisons between Dominants, Intermediates, and Subordinates.

a) Average daily hours spent at supplemental feed, January 1978

Social Class	Mean hours feeding
Dominant	1.65 (S.D. = 1.20)
Intermediate	1.85 (S.D. = 1.68)
Subordinate	1.28 (S.D. = 1.11)

b) Fecal N levels - December, 1977 and March, 1978

Social Class	No. of December Samples	Average % Fecal N	No. of March Samples	Average % Fecal N
Dominant	8	1.60 (S.D.=0.21)	5	1.77 (S.D.=0.12)
Intermediate	10	1.76 (S.D.=0.39)	3	1.62 (S.D.=0.06)
Subordinate	14	1.64 (S.D.=0.11)	5	1.63 (S.D.=0.08)

to that of both Intermediates and Subordinates. Intermediate ewes, however, bedded significantly less than Subordinates. In January, the mean bedding time of Dominants was again similar to that of the others whereas Intermediates bedded significantly longer than Subordinates, the reverse of the situation in October (Table 6).

Although between-class differences were minimal, there were considerable differences between the activity budgets of animals within a given social class. This was particularly true for ewes of intermediate status whose dissimilar grazing or bedding times contributed significantly to the variance of the statistical model in all months tested except February and March. Dominant animals showed significantly variable bedding times in September and February and significantly variable grazing times in November and February. Subordinate animals differed little in their activity patterns, demonstrating only variable grazing times in November and February.

Productivity comparisons

All hypotheses of this study predicting the improved productivity of dominant animals were rejected. Seasonal weight changes in the three social classes did not differ significantly. From October to December, 1977, all classes showed a weight loss of between five and six percent of their October body weights (Table 7). Although subordinates appeared to demonstrate higher average weight gain from March to August than Dominants and Intermediates (33% vs 19% and 17% of March body weights, respectively), the differences were not statistically significant.

A total of five animals died during the 1977-78 winter. Without exception, all animals were over six years of age and severely emaciated. Of the four animals autopsied in detail, all showed advanced stages of gum necrosis and loss of premolars and molars. Although four of the five deaths occurred within the intermediate social class, the frequency of death within each class did not vary significantly from expected values ($Chi^2 = 1.70$, $df = 2$).

The hypothesis that dominant ewes would be reproductively more successful than ewes of lower social rank was rejected on the basis of lamb production in 1978. Of the ten remaining adult ewes comprising the herd in 1978, four were considered dominant, three intermediate, and three subordinate in status. Of these ewes, three dominants, one intermediate and one subordinate produced lambs, with one lamb of the dominant group dying at, or shortly after, birth. While these figures give the impression of a preponderance of reproductively successful dominant ewes, the frequency of lambs from each group did not vary significantly from expected values ($Chi^2 = 0.84$, $df = 2$).

FORAGE AVAILABILITY AND HERD BEHAVIOUR

Ninety plant species were identified in the study site enclosure during the 1977 sampling period (Wikeem and Pitt, pers. comm.). As previously described, the area is dominated by a bluebunch wheatgrass (*Agropyron spicatum*) - big sage (*Artemisia tridentata*) community with

Table 6. Average daylight feeding and bedding times for Dominants, Intermediates and Subordinates(September 1977 to March 1978).

Social Class	Sept Feed (h)	Sept Bed (h)	Oct Feed (h)	Oct Bed (h)	Nov Feed (h)	Nov Bed (h)	Dec Feed (h)	Dec Bed (h)	Jan Feed (h)	Jan Bed (h)	Feb Feed (h)	Feb Bed (h)	Mar Feed (h)	Mar Bed (h)
Dominants	9.26	1.89	7.93	1.45[ab]2	7.69	0.64	5.48	1.40	5.27	2.14[ab]	7.34	1.43	8.52	1.81
	(1.53)1	(0.96)	(0.78)	(0.69)	(0.72)	(0.53)	(1.27)	(1.15)	(1.16)	(0.92)	(1.74)	(1.06)	(0.89)	(1.24)
Intermediates	9.26	1.83	8.11	1.24[a]	7.68	0.29	5.25	1.85	5.0	2.58[a]	7.02	1.37	8.25	2.42
	(1.43)	(0.98)	(1.09)	(0.67)	(0.96)	(0.75)	(1.46)	(1.40)	(1.62)	(1.24)	(1.53)	(0.69)	(0.99)	(0.86)
Subordinates	9.07	1.92	7.93	1.64[b]	7.95	0.87	5.29	1.37	5.61	1.78[b]	7.00	1.65	8.19	2.17
	(1.20)	(0.66)	(0.92)	(0.64)	(0.68)	(0.59)	(1.49)	(1.11)	(0.90)	(0.82)	(1.62)	(1.07)	(0.61)	(0.89)

1 values in parenthesis are standard deviations
2 within a given column, values with different small case letters are significantly different($p < 0.05$)

Table 7. Seasonal weight change comparisons of Dominants, Intermediates and Subordinates.

Social Class	Average weight loss - Oct-Dec 1977 (% of Oct body wt)	Average weight gain - March-Aug, 1978 (% of March weight)
Dominant	5.27 (S.D. = 3.04)	18.97 (S.D. = 2.93)
Intermediate	5.04 (S.D. = 3.31)	17.27 (S.D. = 8.3)
Subordinate	5.63 (S.D. = 4.63)	32.50 (S.D. = 19.16)

grasses contributing more than 40% of the ground cover. Table 8 lists the mean cover values of the major understory plant species determined from 1977 data (from Wikeem, unpubl. data). It should be emphasized that these are mean values for the year and may vary significantly from estimates determined at any particular point in time. Many forbs, for example, are senescent for much of the year, but contribute significantly to the ground cover during the spring growing season.

Of the 90 plant species present, 67 were utilized by the sheep at some period throughout the year at various degrees of intensity (Wikeem, pers. comm.). Diet composition was not always similar to the botanical composition of the area as the sheep demonstrated a high degree of selectivity not only for particular plant species but for plant parts as well (Pitt and Wikeem 1979; Wikeem, pers. comm.).

The seasonal growth cycle for the study area commenced in March with the production of new growth by several plant species. Of the more common grass species, Agropyron spicatum, Bromus tectorum, Koeleria cristata, and Poa secunda were in first or second leaf stages with at least 3 cm of visible growth by mid-March. New leaves were also evident on such forbs as Balsomorhiza sagittata and Achillea millefolium while buds were bursting on browse species including Amelanchier alnifolia and Symphoricarpos albus. Although estimates of diet composition had not been completed for this period of initial growth at the time of this study's completion, a progressive preference towards new growth by the sheep was obvious from ocular reconnaissance of the area's vegetation (Wikeem, pers. comm.).

From late May to late July, 1977, the study area supported its greatest vegetative biomass for the year with the majority of grass, forb, and shrub species passing through their rapid growth phase and progressing into the flowering or fruiting stages. With the availability of a wide range of very palatable and nutritious plants, the sheep demonstrated a high degree of selectivity, generally preferring forbs (Balsamorhiza sagittata, Lupinus sericeus) and shrubs (Amelanchier alnifolia) and selecting against the more common grasses (Bromus tectorum, Agropyron spicatum) (Pitt and Wikeem 1979).

From mid-June to mid-September, the study site experienced the seasonally high temperatures and dry conditions common to this region and the majority of plant species cured at relatively low crude protein levels by late August. Although limited amounts of green foliage were still observed in such common grasses as Agropyron spicatum and Koeleria cristata and such forbs as Eriogonum niveum, Eriogonum heracleoides and Achillea millefolium, most forbs dried and withered into poor forage. With the exception of Artemisia tridentata and Chrysothamnus nauseosus which showed only initial flower development in August, the common shrubs on the study site (Symphoricarpos albus, Amelanchier alnifolia) had formed and dropped their fruit and offered no new leaf development. With the declining availability of forbs and shrubs, the sheep exerted greater foraging pressure on the common grasses, showing less selectivity for particular species but being highly selective for any remaining green growth of Festuca scabrella, Agropyron spicatum and Koeleria cristata, in that order (Wikeem, pers. comm.; pers. observations).

Table 8. Mean cover of the major understory plant species over the 1977 sampling period (from Wikeem, in prep.).

Plant Species	% Cover
GRASSES	
Agropyron spicatum	20.53
Bromus tectorum	10.24
Koeleria cristata	3.63
Stipa comata	3.32
Poa secunda	2.79
Festuca scabrella	trace
FORBS	
Balsamorhiza saqittata	2.16
Eriogonum niveum	1.36
Eriogonum heracleoides	0.94
Achillea millefolium	0.89
Antennaria dimorpha	0.34
Antennaria parviflora	0.26
Lupinus sericeus	0.24
Castilleja thompsonii	0.22
SHRUBS	
Artemisia tridentata	8.07
Symphoricarpos albus	0.65
Chrysothamnus nauseosus	0.57
OTHERS (grasses, forbs, shrubs)	5.89
Total plant cover	62.36
Soil and rock	17.64
Litter	17.18
Total ground cover	97.18

[1] species names from Hitchcock and Cronquist 1973.

From mid-September to mid-November, some regrowth occurred for all of the major perennial bunch grasses, annual grasses (Bromus tectorum, B. mollis), and remaining forbs. By late October, most shrubs had dropped their leaves, although Artemisia tridentata and Chrysothamnus nauseosus were still in the flowering or seed production stage. During this period, the regrowth of the grass species formed the bulk of the sheep's diet, although use of some forbs (Eriogonum niveum, E. heracleoides) also continued (Wikeem, pers. comm.).

From December to February, no significant growth in the vegetation was apparent and the botanical composition of the study area changed little. Green foliage was present throughout this period on many of the common grasses and forbs but was not readily available once the area received a 15 to 30 cm snow cover by late December. The animals exerted their greatest foraging pressure on Agropyron spicatum and Koeleria cristata, cratering for the most recent growth of the plants where possible but utilizing primarily emergent vegetation during the deep snow (> 20 cm) period (e.g. Eriogonum heracleoides, Artemisia tridentata, A. frigida). This diet remained relatively constant until spring growth of grasses and forbs commenced in March. At that time, the sheep were highly selective for this new growth.

Seasonal diurnal patterns

Monthly activity graphs (Fig. 1) demonstrate the seasonal cycle of the herd's diurnal pattern. Each graph contains data from one day considered to be representative for that month. Two days are presented for December to demonstrate the effects of winter storms and snow cover on herd behaviour. The average number of daily activity peaks observed in each month appears on the appropriate graph.

In May and June, the herd members followed a cyclical and synchronous pattern with moderate daily variations. In general, major activity peaks occurred at dawn, mid-morning (0800-1000 h), noon, and late afternoon. The final active period was the most extensive, stretching over four hours from approximately 1600 h to after dark. Cloud bursts would occasionally prompt a brief, unscheduled bedding period in the herd during May. Weather, in general, had little visible effect on the time of onset, duration, or periodicity of activity peaks.

In June, a fifth peak of short duration often occurred at approximately 1400 h and the late afternoon period was bisected by a short bedding session. As a result, a daily average of 5.3 activity peaks was observed in June, compared to only 4.3 in May.

In July, an average of 5.0 peaks occurred each day, but daily variation in diurnal patterns was greater than the previous two months. Active periods were consistently observed at dawn and from late evening to dusk. However, peaks during the interim daylight hours showed a variety of durations and distributions from day to day.

FIGURE 1 Graphs of monthly diurnal patterns of the captive herd (May 1977 to April 1978)

T = mean temperature (°C) for that sampling day. Range of temperatures are given in brackets.

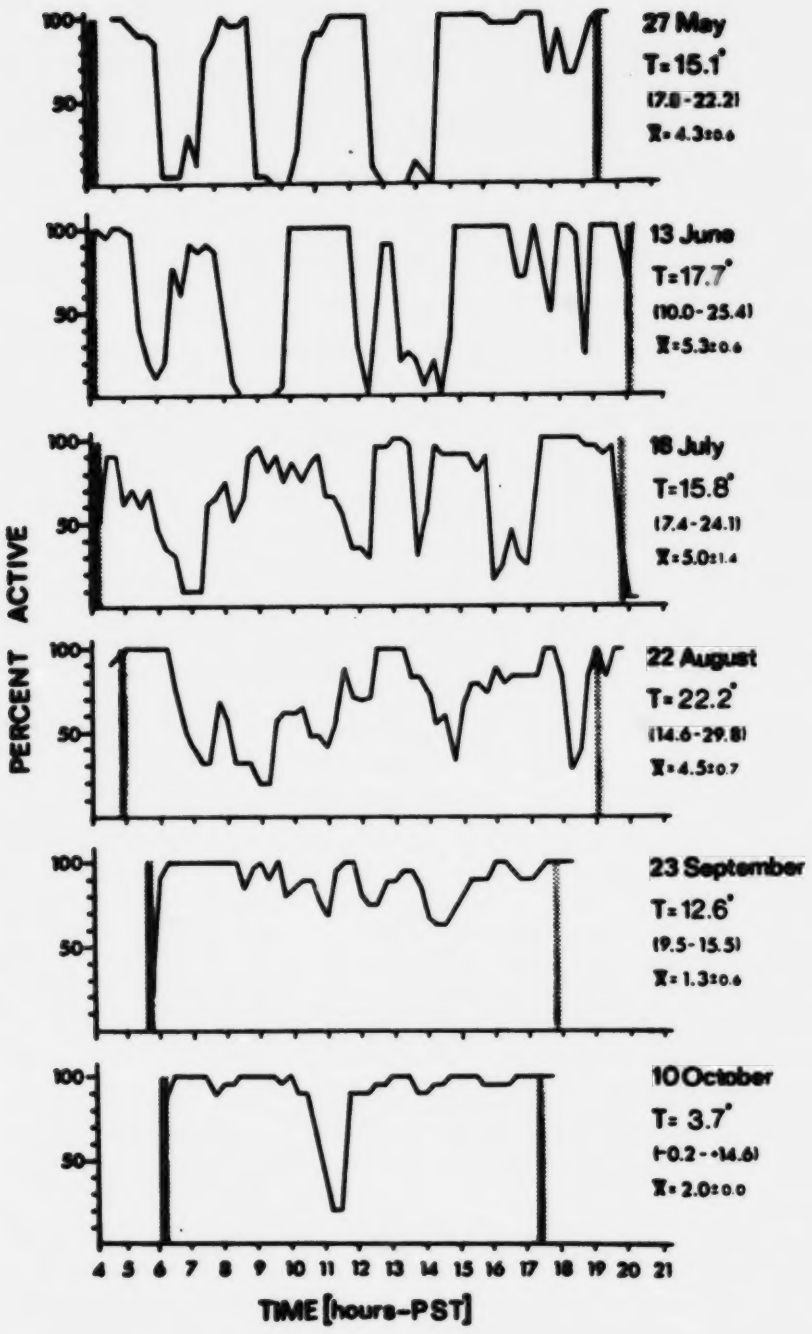
$\bar{x}$ = mean number of daily activity peaks demonstrated for that month.

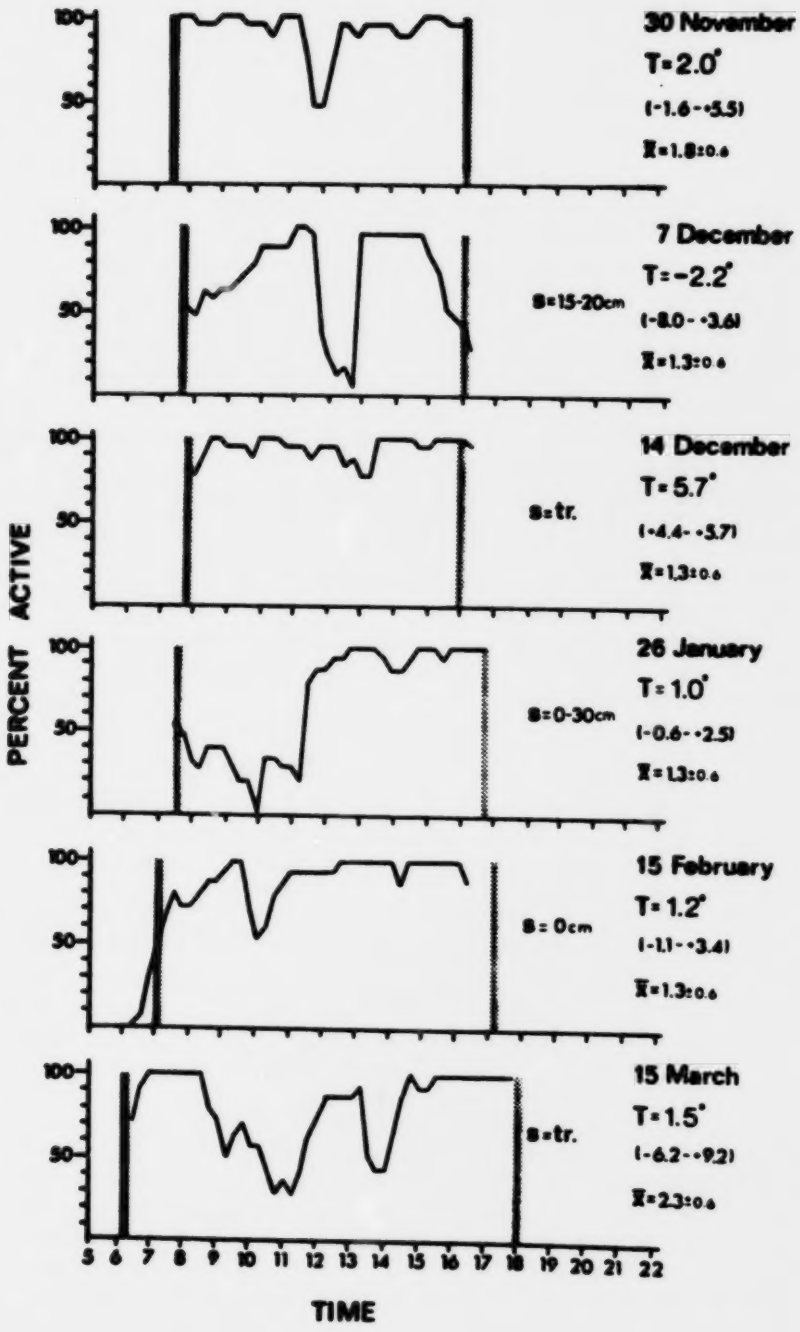
S = range of snow accumulation on the study site.

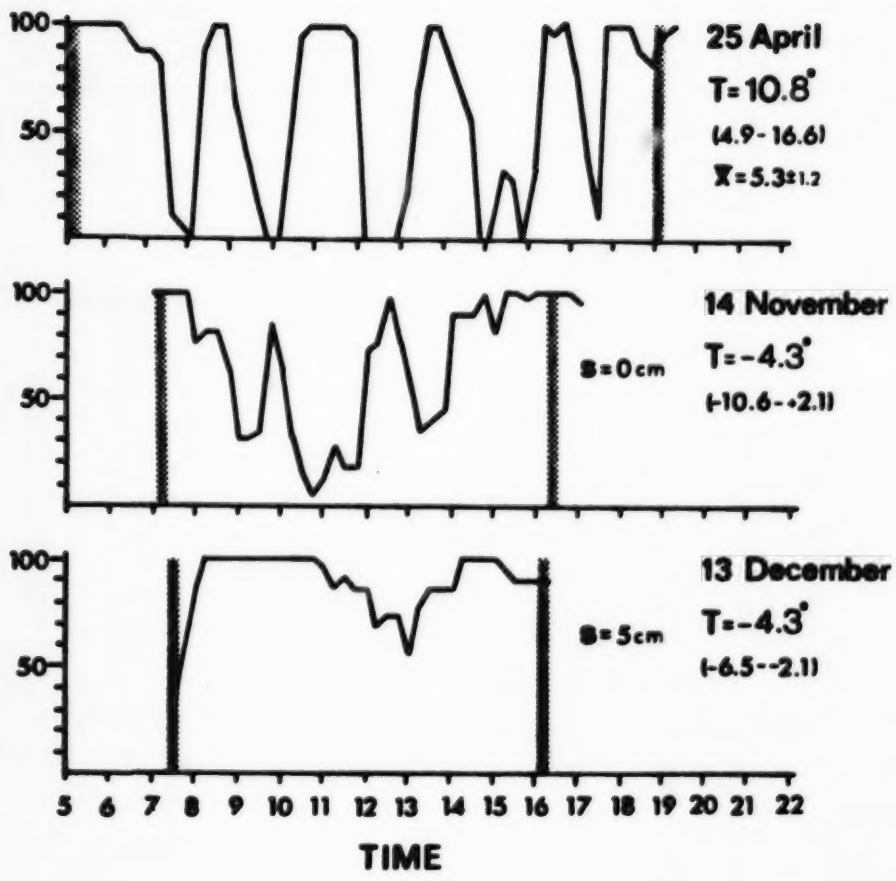
y = percent of the total herd active at each 15 minute sampling interval.

PST = Pacific Standard Time, in hours.

No. of sampling days/month: 3 (Jan., Apr.)
4 (July, Aug., Dec., Mar.)
5 (Sept., Feb.)
6 (June, Oct.)
7 (May, Nov.)


PERCENT ACTIVE
100
50
27 May
T=15.1°
(7.8-22.2)
X=4.3±0.6
13 June
T=17.7°
(10.0-25.4)
X=5.3±0.6
18 July
T=15.8°
(7.4-24.1)
X=5.0±1.4
22 August
T=22.2°
(14.6-29.8)
X=4.5±0.7
23 September
T=12.6°
(9.5-15.5)
X=1.3±0.6
10 October
T=3.7°
(-0.2-+14.6)
X=2.0±0.0
4 5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21
TIME [hours-PST]


30 November
T=2.0°
(-1.6-+5.5)
X=1.8±0.6
7 December
T=-2.2°
(-8.0-+3.6)
X=1.3±0.6
S=15-20cm
14 December
T=5.7°
(-4.4-+5.7)
X=1.3±0.6
S=tr.
26 January
T=1.0°
(-0.6-+2.5)
X=1.3±0.6
S=0-30cm
15 February
T=1.2°
(-1.1-+3.4)
X=1.3±0.6
S=0cm
15 March
T=1.5°
(-6.2-+9.2)
X=2.3±0.6
S=tr.
PERCENT ACTIVE
100
50
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
TIME


100
50
25 April
T=10.8°
(4.9-16.6)
X=5.3±1.2
100
50
S=0cm
14 November
T=-4.3°
(-10.6--2.1)
100
50
S=5cm
13 December
T=-4.3°
(-6.5--2.1)
5 6 7 8 9 10 11 12 13 14 15 16 17 18 19 20 21 22
TIME

August data were the first to show a breakdown in the cyclical diurnal pattern previously observed. An average of 4.5 peaks occurred each day but many of those observed from mid-morning to mid-afternoon were of short durations and involved only slightly more than 50% of the herd. Peaks at dawn and late evening were again always present but varied in length from day to day. Weather during much of June, July, and August was consistently hot and dry. Consequently, no relationship between weather and diurnal patterns could be recognized on a daily basis.

From September to November, the majority of the herd was active at any given time for much of the day. In September, there was no consistent bedding period demonstrated by the herd and, resultantly, the average number of distinct activity peaks dropped to 1.3 per day. In October, an obvious bedding session returned at midday, dividing the daylight active period into two distinct peaks. November data, however, showed a reduced midday inactive period and high activity levels throughout the day. For the first time, some animals were active continuously throughout the daylight hours. The average number of peaks observed per day was 1.67. Although, within each month, weather was variable, there was again no obvious relationship between weather and the animals' diurnal pattern.

In December, the herd demonstrated two entirely different diurnal patterns at different times of the month. The first four days of December were relatively mild (above freezing) with only trace accumulations of snow on the study site. From December 12 to 31, ground accumulations of snow were again minimal with mean daily temperatures dipping slightly below freezing only in late December. In the interim period, however, the study site experienced sub-zero temperatures and a 15 to 20 cm snow cover. The herd reacted to each ambient condition in a different manner. During the mild and/or snow-free periods, herd activity patterns resembled those of November, with the majority of the herd being active throughout the day. The midday bedding period was even less extensive than November. During the seven days of snow accumulations and cold temperatures, a morning peak and an afternoon activity peak were present, with a midday bedding period involving almost the entire herd, separating the two. For the first time in the study, the animals showed significantly reduced activity in the early morning and late evening hours. For December, an average of 1.3 activity peaks was observed per day.

In January, a crusted snow cover of up to 40 cm on higher portions of the study site and slightly sub-zero temperatures (monthly mean of $-2.1^{\circ}C$) were present for much of the month. As previously mentioned, a limited supply of supplemental feed (45 kg of hay per day) was provided for this period in the northeast corner of the study area. In general, the herd would feed at the hay for much of the morning and upon its depletion, move to the lower slopes of the enclosure to forage on the native vegetation for the remainder of the day. Early morning activity was minimal, but herd activity remained high throughout the day once foraging was initiated, usually by late morning (1100 h). Data from only one observation day showed a significant degree of mid-morning foraging and a synchronous bedding period before the normal late morning to dusk activity peak ($\bar{x}$ = 1.3 peaks/day).

In February, snow accumulation rapidly declined on lower slopes and the herd was again dependent solely on the mature vegetation of the study site. Although an avoidance of early morning hours by the animals was no longer pronounced, the herd showed little difference in its diurnal pattern from January for the remainder of the day. The majority of the animals began foraging at or slightly before 0800 h and, in general, remained active throughout the day from that time on. As in January, an average of 1.3 activity peaks per day was observed.

March data showed the return of multiple active and bedding periods during the daylight hours. An activity peak was once again consistently observed at dawn and a second, more extensive one stretched from late morning to dusk. Although the only major bedding session occurred at mid-to late morning, a second inactive period, varying in duration and degree of herd member participation, was frequently observed between 1300 and 1500 h. The average number of activity peaks observed per day increased from February's value of 1.3 to 2.3 in March.

In April, the herd members were extremely synchronous and cyclic in their activity patterns, similar to that observed in May and June of the previous year. The herd would frequently transfer from an active, foraging state to one of complete inactivity in the interval between two consecutive scan sampling observations (15 min). Consistent peaks occurred at dawn, late afternoon (1600 h), and evening to dusk while interim activity periods varied daily in distribution and duration. An average of 5.3 peaks was observed per sampling day.

Although intensive field observations for this study ended on June 30, 1978, additional herd activity data were collected on November 14, 1978 and December 17, 1978 during brief visits to the study site (Fig. 1). This enabled the herd's diurnal pattern to be determined after a growing season in which grazing pressure had been reduced considerably from the previous year.

On November 14, weather conditions were seasonal, with clear skies and daylight temperatures ranging from -3°C to 0°C. The study area had not received snow to that date. Four activity peaks were observed, the two most extensive occurring from dawn to early morning (0900 h) and from late afternoon (1800 h) to dusk. Two additional peaks were observed at 0945 h and 1230 h. This pattern varied considerably from that demonstrated in November, 1977, where the majority of the herd was active at any given time for most of the day.

On December 13, 1978, a 5 cm snow cover and slightly sub-zero temperatures made ambient conditions similar to those present during the stormy period of December, 1977. However, the herd's diurnal pattern resembled that observed on milder, snow-free days of the previous December. Activity was reduced only slightly in the early morning and late evening, and the majority of the herd was active at any given time throughout the entire day. Some inactivity was obvious at midday but involved only 45% of the herd at its peak period.

Nocturnal activity

The degree of nocturnal activity of the herd varied considerably with the time of year. On May 5 and June 20, 1978, the herd was observed from dusk to 2400 h Pacific Standard Time (PST) under clear skies and moonlit conditions. Lighting was considered to be at a minimal level (animals were no longer visible without the spot lamp) by 1930 h and 2115 h PST, respectively. On both occasions, the herd seemed to continue the cyclic grazing/bedding pattern established during the daylight hours of these months, although active periods were less extensive and involved fewer animals. The entire herd on May 5 was bedded by 2008 h, approximately 38 minutes after complete darkness. With the exception of minor shuffling of bedding sites, there was no activity from this time to 2210 h, when four animals began foraging. A limited activity peak involving only four to six animals at a time continued for the remainder of the observation period. During this time, foraging was restricted to the immediate vicinity of the bedding area. On June 20, the herd was completely bedded by 2100 h, 15 minutes before the area was considered to be in complete darkness, and the herd remained inactive until 2235 h. At that time, a foraging bout was initiated by three animals, culminating in an activity peak which involved all but five herd members. Similar to May 5 observations, the grazing animals remained within 50 m of the bedding area. By 2319 h, all animals had rebedded and continued to do so for the rest of the observation period.

On November 14, 1978, during the rutting period, the herd was monitored from dusk to 2100 h (PST) in clear moonlit conditions and slightly sub-zero temperatures. Although initial signs of bedding were observed at 1702 h, 15 minutes before the area experienced its minimum light levels for the night, bedding was not extensive for almost an hour because of the continued harassment of ewes by courting rams. By 1755 h, 13 of the 26 herd members were still active and remained so until 1830 h when all but seven animals bedded. The entire herd finally became inactive at 1905 h and no foraging or courtship behaviour was observed for the rest of the monitoring period. At dawn the following morning, only eight of the herd members had moved a significant distance (> 100 m) during the night, indicating limited nocturnal movement.

On December 13, night observations were recorded from dusk to 2000 h under a low overcast sky and $-3^{\circ}C$ temperatures. The study area was blanketed by approximately 15 cm of fresh snow. Bedding activity was initiated by the animals at 1605 h, approximately 40 minutes before total darkness and progressed gradually until the entire herd was bedded by 1745 h. With the exception of occasional shifts in bedding sites, the herd remained stationary throughout the observation period.

During scan sampling in December, 1977 and January, 1978, observations at dusk and dawn of successive sampling days showed, with rare exceptions, no movement in the animals overnight, suggesting that night movement during the colder months is more restricted than during more temperate seasons.

Seasonal activity budgets

Average daylight hours devoted to feeding by the herd members ranged from 5.32 h/sample day and 5.27 h/sample day for December and January, respectively, to 9.22 h in September (Table 9). However, means for the remaining months showed no consistent trend and were all within one hour of the yearly mean of 7.43 h/sample day, resulting in an insignificant correlation between feeding time and daylength ($r = 0.51$).

Regardless of a mid-winter increase in daily bedding time, the average number of daylight hours devoted to bedding proved to be significantly correlated to daylength ($r = 0.92$), peaking at 5.75 h/sample day in June and decreasing monthly to 0.77 h/sample day in November. Although December and January values increased irregularly to 1.6 and 2.2 h/sample day, respectively, the bedding times began an orderly monthly climb from 1.47 h/sample day in February to 5.51 h/sample day in May. The yearly average was 3.0 h/sample day.

Daily travel time showed no obvious seasonal pattern during the year. Values ranged from 1.69 h/sample day (April) to 0.36 h/sample day in March and were not significantly correlated to daylength ($r = 0.51$). Relatively high values also occurred in May (0.97 h/sample day) and July - August (1.03 h/sample day).

Daily standing time, also not significantly correlated to daylength ($r = 0.24$), showed two peaks during the study year, with the highest values occurring in the hottest and coldest months of the year (June to August and January to February, respectively). During these periods, standing times remained at or slightly above 1 h/sample day. For the remaining months, values fluctuated between 0.42 h/sample day (Nov.) and 0.91 h/sample day (April).

Time devoted to "other" activities (playing, interacting, maternal behaviour) during the daylight hours proved to be significantly correlated to daylength ($r = 0.85$), peaking in May, June, and July (0.46, 0.65, and 0.42 h/sample day, respectively) and then dropping gradually to a low of 0.10 h/sample day in February. Values began increasing in the spring, reaching 0.19 h/sample day by April 1978.

Because daylengths varied considerably on a seasonal basis, actual daylight activity times provided marginally useful and sometimes deceptive information on the seasonal trends of these activities. Consequently, the proportions of sampling days devoted to various activities were calculated to provide a more standardized set of values.

Unlike actual feeding times, the proportion of daylight hours spent foraging varied dramatically between seasons. Values increased in an orderly fashion from April (49%) to November (81%), dropped to 62 and 55% in December and January, respectively, and then climbed in February and March to 70 and 78%, respectively.

Table 9. Average daylight activity budgets of the adult ewes, by month.

Month	days/ month	Mean length of sampling days (h)	Feeding time(h)	% of day length	Bedding time(h)	% of day length	Travel time (h)	% of day length	Standing time (h)	% of day length	"Other" time (h)	% of day length
May	7	15.00 (0.0)[1]	7.40 (0.87)	49.3	5.51 (0.60)	36.7	0.97 (0.41)	6.5	0.67 (0.49)	4.5	0.46 (0.37)	3.1
June	6	16.04 (0.70)	7.90 (1.13)	49.3	5.75 (1.03)	35.8	0.64 (0.36)	4.0	1.09 (0.80)	6.8	0.65 (0.41)	4.1
July-Aug.	8	16.21 (0.59)	8.38 (1.05)	51.7	5.39 (0.97)	33.2	1.03 (0.51)	6.4	0.99 (0.65)	6.1	0.42 (0.33)	2.6
September	5	12.70 (0.48)	9.22 (1.40)	72.6	1.85 (0.89)	14.6	0.72 (0.48)	5.7	0.58 (0.39)	4.6	0.33 (0.30)	2.6
October	6	10.75 (0.42)	8.03 (0.98)	74.7	1.37 (0.67)	12.7	0.60 (0.48)	5.6	0.58 (0.48)	5.4	0.17 (0.25)	1.6
November	7	9.39 (0.49)	7.65 (0.84)	81.5	0.77 (0.69)	8.2	0.40 (0.29)	4.3	0.42 (0.34)	4.5	0.13 (0.20)	1.4
December	4	8.56 (0.24)	5.32 (1.39)	62.1	1.60 (1.30)	18.7	0.81 (0.47)	9.4	0.73 (0.56)	8.5	0.13 (0.20)	1.5
January	3	9.5 (0.00)	5.27 (1.28)	55.5	2.20 (1.04)	23.2	0.71 (0.37)	7.5	1.22 (0.61)	12.8	0.11 (0.20)	1.2
February	5	10.25 (0.40)	7.14 (1.62)	69.7	1.47 (0.95)	14.3	0.46 (0.36)	4.5	1.07 (0.84)	10.4	0.10 (0.16)	1.0
March	4	11.44 (0.59)	8.33 (0.80)	72.8	2.10 (1.04)	18.4	0.36 (0.27)	3.1	0.49 (0.28)	4.3	0.14 (0.26)	1.2
April	3	14.52 (0.14)	7.13 (0.94)	49.1	4.61 (0.83)	31.7	1.69 (0.85)	11.6	0.91 (0.47)	6.3	0.19 (0.24)	1.3
		$\bar{x}$ = 12.21	$\bar{x}$ = 7.43 r = 0.51[2]		$\bar{x}$ = 3.0 r = 0.92*		$\bar{x}$ = 0.76 r = 0.51		$\bar{x}$ = 0.80 r = 0.24		$\bar{x}$ = 0.26 r = 0.85*	
Nov. '78 (1 day)		$\bar{x}$ = 9.75	$\bar{x}$ = 5.42 (0.76)	55.6	$\bar{x}$ = 3.04 (0.57)	31.1	$\bar{x}$ = 0.44 (0.25)	4.52	$\bar{x}$ = 0.75 (0.41)	7.70	$\bar{x}$ = 0.10 (0.13)	1.14
Dec. '78 (1 day)		$\bar{x}$ = 9.0	$\bar{x}$ = 6.33 (0.55)	70.3	$\bar{x}$ = 1.23 (0.60)	13.7	$\bar{x}$ = 0.55 (0.50)	6.1	$\bar{x}$ = 0.96 (0.58)	9.6	$\bar{x}$ = 0.03 (0.09)	0.3

[1] values in parenthesis are standard deviations
[2] correlation coefficient (with daylength)
* significant correlation ($p < 0.05$)

Bedding proportions generally followed a reverse trend to that of feeding, declining from peak spring values (32% in April, 37% in May) to only 8% in November. Winter bedding proportions increased to 19% and 23% in December and January, respectively, and then dropped to 14% and 18% in February and March, respectively.

The proportion of daylength devoted to travel showed no seasonal trend, ranging between values of 3% to 7% for the months of May to November inclusive, January, February, and March. Travel time proportions peaked in April (12%) with relatively high values also occurring in December (9%).

Standing time proportions also showed no seasonal trend. Relatively high values occurred in January (13%), December (9%), and February (10%), with values for the remaining months fluctuating between 4% (March) and 7% (June). Unlike actual standing times/sample day, standing time proportions did not demonstrate a secondary peak in summer.

The proportion of daylength devoted to "other" activities followed a similar pattern to actual times. Peak values occurred in May (3%) and June (4%), declined in a gradual fashion to 1% in February, and then increased slightly in March and April.

The herd's diurnal budget varied considerably on sampling days in November and December 1978 from that demonstrated during a comparable period in 1977. Although times devoted to travelling, standing, and "other" activities on November 14, 1978 were not unlike the mean daily values for November, 1977, the herd reduced their grazing time and increased their bedding time by more than two hours from 1977 values. Times devoted to standing, travelling, and "other" activities also varied only slightly between December 1977 and 1978 sampling days. However, during inclement weather on December 13, 1978, time spent grazing increased by more than one hour over the December 1977 mean daily value, while bedding time decreased by approximately 0.4 h. Of the total average grazing time demonstrated by the herd in 1978, 0.8 h was devoted to digging for forage. This varied considerably from 1977, when digging times averaged 0.2 h/sample day during snow accumulations of December, and 0 h/sample day once mild temperatures removed much of the snow cover in late December.

In addition to these seasonal changes in the herd's activity budget, daily fluctuations were also evident. As described in Methods, the linear model used statistically to assess between-group differences in grazing and bedding times also assessed the effects of sampling day and the sampling day - social group interaction term. Although the interaction term contributed no significant variance to the statistical model, there was significant day to day variation in the herd's activity budget for most months of the year. May to September inclusive, December, and February were months in which significant day to day fluctuations were present in the times devoted to all five activity categories. In October, November, and April, all but one activity (standing, standing, and "other", respectively) showed significant daily variation in duration, while in

March, bedding alone varied daily. January was the only month in which the herd's activity budget was consistent from day to day.

EFFECTS OF PHYSIOLOGICAL CONDITION ON DAILY ACTIVITY BUDGETS

As previously described in Results, only ewes of dominant and intermediate status died during the winter. Therefore, comparisons of grazing and bedding times of healthy and sick animals in October, November, and December were possible only within these two social classes.

Among the dominant animals, no significant differences existed between the grazing or bedding times of sick and healthy animals for any of the three months tested. However, differences were evident within the intermediate class of animals (Table 10a). In October, sick animals grazed significantly ($p < 0.05$) longer than healthy animals, although bedding times were similar for the two groups. In December, just prior to the majority of deaths, grazing times were similar but sick animals bedded significantly longer than healthy animals ($p < 0.05$).

In March and April, ewes from each of the three social classes were supporting late stages of fetal development, enabling grazing and bedding times of pregnant and non-pregnant ewes to be compared within each class (Table 10b). Pregnancy demands did not appear to alter activity budgets appreciably, and no significant differences were detected between the social groups. However, within every class, pregnant ewes in April did demonstrate longer grazing times than non-pregnant ewes, but not significantly so.

ENERGY EXPENDITURE ESTIMATES FOR ADULT EWES

The estimated mean basal metabolic rate (BMR) for the adult ewes demonstrated no clear seasonal trends, other than an elevated level in the spring relative to other periods of the year (Table 11). BMR's reached 1.53 and 1.60 kcal/kg/h in May and June, respectively, dropping to a yearly low of 0.93 kcal/kg/h in the July - August and September periods. Values ranged irregularly between 1.18 and 1.06 kcal/kg/h from October to February, before demonstrating increased early spring levels of 1.50 and 1.49 kcal/kg/h in March and April, respectively.

Estimates of the average hourly energy expended by the herd members during a typical daylight routine followed a similar pattern to BMR's (Table 12). Values peaked in April, May, and June (2.29, 2.39, 2.29 kcal/kg/h, respectively), dropped to yearly lows of 1.52 and 1.54 kcal/kg/h in the July - August and September periods, respectively, and then ranged irregularly between 1.83 and 1.61 kcal/kg/h from October to February. In March, the activity cost increased considerably to 2.04 kcal/kg/h. With the inclusion of pregnancy costs, April's value climbed to 2.47 kcal/kg/h. Lactation costs increased May's value to 3.13 kcal/kg/h.

Table 10a. Average grazing and bedding times of healthy and sick ewes (October to December 1977), in hours.

	Dominants						Intermediates					
	Feed. times			Bed. times			Feed. times			Bed. times		
	Oct.	Nov.	Dec.	Oct.	Nov.	Dec.	Oct.	Nov.	Dec.	Oct.	Nov.	Dec.
Healthy	8.10	7.82	5.28	1.48	0.55	1.38	7.78[a1]	7.29	5.48	1.11	0.66	1.21[a]
Sick	7.75	7.56	5.69	1.42	0.73	1.44	8.32[b]	7.67	5.08	1.32	0.87	2.28[b]

[1] within any given column, values with different small case letters are significantly different ($p<0.5$)

Table 10b. Average grazing and bedding times of pregnant and non-pregnant ewes (March, April 1978), in hours.

	Dominants				Intermediates				Subordinates			
	Feed. times		Bed. times		Feed. times		Bed. times		Feed. times		Bed. times	
	Mar.	Apr.	Mar.	Apr.	Mar.	Apr.	Mar.	Apr.	Mar.	Apr.	Mar.	Apr.
Pregnant	8.42	7.49	1.73	4.42	8.00	7.58	2.13	5.00	8.71	7.33	1.94	4.58
Non-pregnant	8.81	7.08	2.06	4.50	8.37	6.87	2.56	4.83	8.06	6.50	2.28	4.54

Table 11. Average estimated basal metabolic rates for adult ewes, by month.

Month	Grand Mean (kcal/day)	Sex Factor (+)	Seasonal Factor	Nutritional Factor	Trial Temp. Factor	Ambient Temp. Factor	Body Wt. Factor	FMR kcal/day	Minus Standing Increment	BMR kcal/day	BMR kcal/kg/h
May	2 631.87	- 117.45	864.13	- 237.37 (fasted)	- 90.14 (10.7°C)[2]	- 359.57 (12.0°C)[4]	- 190 (59.5kg)[5]	2 501	- 314	2 187	1.53
June	2 631.87	- 117.45	864.13	- 237.37	0.00[3] (17.1°C)	- 359.57 (18.8°C)	- 235[6] (58.0kg)	2 546	- 314	2 241	1.60
July-Aug	2 631.87	- 117.45	- 93.23[1]	- 237.37	0.0 (20.3°C)	- 359.57 (20.5°C)	- 290 (56.0kg)	1 534	- 296	1 238	0.93
September	2 631.87	- 117.45	- 93.23	- 237.37	0.0 (12.9°C)	- 359.57 (13.8°C)	- 340 (54.0kg)	1 484	- 285	1 199	0.93
October	2 631.87	- 117.45	- 93.23	- 237.37	- 90.14 (8.7°C)	+ 56.59 (8.5°C)	- 380 (52.5kg)	1 770	- 277	1 493	1.18
November	2 631.87	- 117.45	-250.43	- 237.37	- 90.14 (3.5°C)	+ 56.59 (2.0°C)	- 400 (52.0kg)	1 593	- 275	1 318	1.06
December	2 631.87	- 117.45	-250.43	- 237.37	- 28.24 (-1.9°C)	+ 56.59 (-1.8°C)	- 430 (50.7kg)	1 625	- 268	1 357	1.12
January	2 631.87	- 117.45	-250.43	- 237.37	- 90.14 (1.1°C)	+ 56.59 (-2.1°C)	- 450 (50.0kg)	1 543	- 264	1 277	1.06
February	2 631.87	- 117.45	-250.43	- 237.37	- 90.14 (0.7°C)	+ 56.59 (1.0°C)	- 480 (49.0kg)	1 513	- 259	1 254	1.06
March	2 631.87	- 117.45	-240.10	- 237.37	- 90.14 (5.0°C)	+ 56.59 (5.5°C)	- 500 (48.0kg)	1 984	- 253	1 731	1.50
April	2 631.87	- 117.45	-240.10	- 237.37	- 90.14	+ 56.59	- 480	2 004	- 259	1 745	1.49

1 Chappel's (1978) Aug. to Oct. Correction factor used for July-Aug. period of this study.
2 Temperatures in parentheses represent mean temperatures of sampling days for each month.
3 Trial temp. factors are not available for temperatures above 10°C based on Chappels' suggestion that the bighorn thermo-neutral zone does not extend much above 10°C, an increase in the trial temp. factor to 0.0 was arbitrarily chosen for the 10 - 20°C range.
4 Temperatures in parentheses represent mean monthly temperatures.
5 Weights in parentheses represent mean body weights of adult ewes.
6 Body weight factors have been interpolated or extrapolated from Figure 5.5 (Chappel 1978), based on Chappels' suggestion that metabolic rate was almost linearly related to body weight.

Table 12. Average estimated daylight energy expenditures for adult cows, by month.

Activity	May		June		July-Aug.		September		October		November		December		January		February		March		April	
	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	% of Total	Energy Expended (kcal/sample day)	
Grazing	863	40.5	932	43.6	638	46.4	675	63.7	678	66.3	592	73.8	420	52.7	393	50.6	522	64.5	770	68.7	670	
Bed-Rum.	580	27.2	615	28.7	353	25.7	116	11.0	102	10.0	52	6.5	111	13.9	143	18.4	94	11.6	181	16.2	391	
Walking (5km/hr)	163	7.7	143	6.7	200	14.6	134	12.7	113	11.0	71	8.9	155	19.4	140	18.0	85	10.5	70	6.2	309	
Running	287	13.5	92	4.3	33	2.4	32	3.0	45	4.4	30	3.7	31	3.9	0.0	0.0	19	2.4	13	1.2	131	
Standing	70	3.3	115	5.4	64	4.7	36	3.4	43	4.2	28	3.5	50	6.3	78	10.0	67	8.3	40	3.6	78	
Other	167	7.8	242	11.3	87	6.3	66	6.2	42	4.1	29	3.6	30	3.8	23	3.0	21	2.6	46	4.1	99	
Total Daylight Expenditures (Kcal/sample day)	2 130	100	2 139	100	1 375	100	1 059	100	1 023	100	802	100	797	100	777	100	808	100	1 120	100	1 428	
(Kcal/kg/hr)	2.39 (3.13)[1]	-	2.29	-	1.52	-	1.54	-	1.81		1.63	-	1.83	-	1.64	-	1.61	-	2.04	-	2.29 (2.47)[2]	
BMR (Kcal/kg/hr)	1.53	-	1.60	-	0.93	-	0.93	-	1.18		1.06	-	1.12	-	1.06	-	1.06	-	1.50	-	1.49	
Multiple of BMR	1.56	-	1.43	-	1.63	-	1.66	-	1.53	-	1.54	-	1.63	-	1.55	-	1.52	-	1.36	-	1.53	

[1]Activity costs with peak lactation costs included.
[2]Activity costs with peak pregnancy costs included.

When expressed as multiples of BMR, average daily activity costs demonstrated irregular but limited monthly fluctuations (Table 12). Normal daylight behaviour proved to be slightly more expensive relative to BMR in July - August (1.63 x BMR), September (1.67 x BMR), and December (1.63 x BMR), and least expensive in June (1.43 x BMR) and March (1.36 x BMR). Multiples ranged between 1.52 and 1.56 in the remaining months.

DISCUSSION

SOCIAL ORGANIZATION

Dominance hierarchy in the herd

The social behavioural repertoire of the adult ewes was considerably less than that described previously for adult rams. Of the 17 behavioural patterns of rams described by Geist (1971), only eight were performed by females in this study; absent were patterns involving horn displays. That bighorn ewes would have relatively few horn displays is not surprising, considering the limited variability in horn size of adults. Geist (1971) suggested that rams can assess a strange ram's social status by the latter's horn size and, as a result, horn displays have evolved as a non-violent means of exhibiting social status. However, amongst ewes, such displays would have little value because of the often indistinguishable differences in their horn sizes. In most ungulate societies where horn or antler sizes of adults show only subtle differences, behaviour patterns which exaggerate body rather than horn development are more pronounced (mountain goat (Oreamnos americanus), Geist 1964; East African buffalo (Syncerus caffer), Sinclair 1974). It is also possible that, in relatively small, consistent groups of animals such as the captive herd, individual recognition develops between herd members (Shackleton 1973), thus eliminating the need for many social displays once a hierarchy has been established.

Two additional patterns, horn wrestling (Shackleton 1973) and squat-urination by subordinates, similar to the urination response of oestrus and anoestrus females to aggressive males, described by Geist (1971) were also observed for the ewes. Horn wrestling appeared to be an extension of the clash, impossible in large rams where basal horn diameters would prevent interlocking. The urination response of subordinate ewes was directed both at dominant ewes and rams after aggressive approaches by these animals. Dominant ewes, once confronted by this posture, would show no further aggression towards the subordinate.

The infrequent occurrence of social interactions between the captive ewes is a behavioural quality not uncommon for female ungulate societies. Such a social strategy is biologically sound, considering a female's bioenergetic constraints. To maximize her reproductive success, an ewe must minimize energy expenditures on activities not vital to maintenance or to her reproductive effort (Geist 1971). Since interactions, particularly prolonged dominance disputes and play, are energetically very costly and occasionally damaging, these activities within the female

society should be greatly reduced in number and duration, compared with those of males. Such a reaction was clearly evident among the captive animals. The two-year old ram in the herd initiated 67% more aggressive interactions with the single yearling male herd member from June to December 1977 than the most aggressive adult ewe initiated with 14 potential adult ewe opponents during the same period of time. In addition, ewes did not exhibit any ritualized dominance fights, as did the rams, and restricted their playlike activities to late spring and summer months when their physiological and foraging conditions were at an optimum annual level.

Reduced aggression amongst females in comparison to males has been reported for several ungulate species, including roan antelope (Hippotragus equinus, Joubert 1974) and oryx (Oryx beisa, Walther 1978). The rarity of actual dominance fights between female mountain sheep has also been reported by Geist (1971) and Blood (1963).

That the captive ewes could successfully coexist with such a quiescent social structure was probably the result of resource availability. Hierarchies often function as a relatively efficient means of resource allocation but vary in their rigidity depending on the supply and distribution of resources. Rigid hierarchies would be expected with limited, localized resources. Forage and rams were the two most significant resources which the ewes required for maintenance and reproductive success, respectively. However, ewes were bred regardless of their social status, negating the need for dominance disputes amongst the ewes to attain breeding privileges. Forage, in turn, was distributed relatively homogeneously over the study area for much of the fall, winter, and early spring periods. Geist (1974) suggests that "dispersed and diffused food of low density per unit area will lead to a selection against food competition by overt aggression...." Consequently, it can be speculated that the captive sheep, by exploiting a relatively dispersed food resource, were able to coexist with a minimum of forage disputes. This was particularly true after the range plants had cured to a low nutritive state and the animals were dispersed to their greatest degree during foraging bouts. Conversely, feeding disputes became more frequent when the animals were dependent upon "point" or localized resources, such as the water trough and supplemental hay.

The preponderance of bedding disputes likely resulted from the repeated use by the herd members of one of several, apparently preferred, bed sites during major resting periods. This behaviour concentrated animals into localized areas, creating a situation conducive to social confrontations and eventual interactions. It is doubtful that an actual shortage of bedding sites initiated these bedding disputes.

The relative abundance of positional disputes appeared to result from crowding by the herd, artificially enhanced by their captive state, rather than a lack of space. Invariably, a foraging drive would be interrupted by the perimeter fence of the enclosure, causing the animals to cluster momentarily before redirecting their feeding effort. This crowding would frequently initiate a burst of social interactions as individual distances were being violated.

In all probability, the absence of a biological requirement for a rigid hierarchy (i.e. localized, limited resource) was largely responsible for the non-linear and somewhat disorganized hierarchy of the captive herd. Enforcing a rigid hierarchy without definite resource gains would have been energetically wasteful. However, additional factors may also have contributed to the hierarchy's non-linearity. Dominance reversals and triangles are often a temporary instability common to a new assemblage of animals (Wilson 1975). When first trapped, the captive herd was comprised of animals of at least two and possibly several different maternal groups which previously may not have mutually interacted. Therefore, confined to a common area, many of these animals had no relative status to each other and the hierarchy was initially unclear. In December and January, winter mortalities forced even more dominance reorganization, possibly explaining the continued low linearity of the hierarchy in 1978.

Size of the herd is an equally plausible explanation for the hierarchy's non-linearity. Certain animal societies have an inherent critical herd or flock size, above which their hierarchies demonstrate non-linear tendencies (Schjelderup-Ebbe 1922, Allee 1952, cited in Wilson 1975). It is possible that the original size of the captive herd (16 adults) was too large for a straight line hierarchy to develop. Blood's (1963) and Shackleton's (1973) data, which showed the average maternal group size of bighorns including lambs and yearlings to be substantially less than 16 animals for much of the year, add support to the suggestion that, socially, the captive group was unusually large.

Behavioural studies on other ungulate societies have resulted in a variety of findings on social hierarchies. Bighorn rams have a strongly linear hierarchy (Geist 1971), but spend the majority of the year in relatively small, cohesive bands of less than ten animals (Blood 1963; Shackleton 1973; personal observations). It is not known if similar straight line hierarchies develop in larger bands of males which can exist temporarily. Linearity has also been reported for the hierarchies of domestic cattle (Schein and Fohrman 1955), adult cow and bull Roosevelt elk ((Cervus elaphus roosevelti) Lieb 1968; Franklin et al. 1975), mixed herds of roan antelope (Joubert 1974), pronghorns (Kitchen 1974), and adult bull East African buffalo (Sinclair 1974). Unfortunately, the strength of the linearity is not expressed (e.g. Landau's index of linearity, from Wilson 1975) in many of these studies, making assessment of their findings difficult. The majority of ungulate studies show variable degrees of linearity in the hierarchies with prominent dominance triangles and dominance reversals (domestic cattle, Wagnon et al. 1966; reindeer, Espmark 1974b; roe deer, Espmark 1974b; American bison (Bison bison), Lott 1974; adult cow East African buffalo, Grimsdell 1969, cited in Sinclair 1974), similar to the findings of this study.

Given free ranging conditions and a more natural group size and age composition, it is possible that cohesive maternal bands of bighorn sheep develop a linear hierarchy. However, considering that these animals traditionally exploit a relatively dispersed resource and must govern themselves behaviourally because of energetic constraints, it can be postulated that dominance in the group would not be any more rigidly enforced or evident than it was within the captive animals.

Stability of herd's social system

Relative stability is a required characteristic of a hierarchy if such a social system is to be energetically beneficial to its participants. Hierarchies presumably enable conspecifics to coexist as a social unit with a minimum of costly aggressive interactions over resource allotment (Geist 1971; Wilson 1975). An unstable dominance system would result in dominance disputes and frequent fights, thus losing its energy conserving qualities. Not surprisingly, the captive herd demonstrated only minor dominance shuffling during the 14-month study, in spite of the herd reduction in December and January. The two animals which showed increases in their dominance values and relative positions in the hierarchy did so just prior to or after the birth of their lambs. Considering that only five lambs were produced that year (two of them to previously established dominants), the presence of lambs may have been a contributing factor to the ewes' rise in status.

Hierarchy stability has been widely documented for many ungulate species, including dairy heifers (Beilharz and Mylrea 1963), domestic goats, Capra hircus (Ross and Berg 1956), Roosevelt elk calves (Lieb 1968; Franklin et al. 1975) and roan antelope (Joubert 1974). Scott (1958) suggests that linear hierarchies are relatively stable and permanent, presumably "due to the drastic and long lasting emotional responses connected with fighting and avoidance...." However, similar to this study, dominance shuffling has been reported where members of a hierarchy experience morphological or physiological changes. Espmark (1964) showed that the social status of reindeer declined upon the loss of their antlers. He also suggested that pregnant cows or cows with calves will have a relatively high social rank and will attain the feeding privileges of dominants needed in times of food shortages to meet reproductive demands. Similarly, Miller (1971, 1974) found pregnant blacktail deer (Odocoileus hemionus columbianus) became more aggressive once their fawns were born, often dominating previously dominant animals.

Established hierarchies will often show temporary instability and increased internal aggression with the introduction of "strange" animals to the herd, as these animals attain their respective social ranks (Wilson 1975). Such xenophobic tendencies were not expressed by the captive herd when an ewe from the Game Farm paddock entered the study area unexpectedly. Consequently, the herd's hierarchy, in addition to being loosely maintained, was a relatively open system enabling the uneventful passage of animals into or out of the group. Such a system is highly desirable in animals which, like sheep, often concentrate with unfamiliar conspecifics on localized winter ranges for several months of the year. Aggression at this time would mean a costly energy expenditure at a time of limited energy reserves.

Xenophobic tendencies are usually pronounced in tight-knit, rigidly structured groups typical of many species of birds (domestic chickens, Wilson 1975), primates (rhesus monkeys, Macacca mulatta, Southwick 1969, cited in Wilson 1975), and canids (wolf, Canis lupus, Mech 1970). They have also been reported for some ungulate species including roan antelope (Joubert 1974) and male oryx (Walther 1978). However, in most free

ranging ungulate societies, the social systems are relatively open, similar to the captive bighorn herd, and new animals are permitted to join established herds with little aggression arising (e.g. caribou, Bergerud 1974).

Determinants of dominance

Most behavioural studies which have attempted to elucidate the determinants or consequences of dominance have been faced with constructing hierarchies from incomplete interaction matrices (i.e., where interactions between all possible pairs of herd members were not observed). Consequently, dominance values have generally been determined for study animals from the proportion of opponents each animal dominates. The herd members are then ranked according to these values. The relationship of rank to various parameters has been assessed non-parametrically by rank correlation methods (Kruskal and Wallis method, in Wagnon et al. 1966). More commonly, the dominance values are transformed into angles which are normally distributed and which enable correlation coefficients between dominance values and various parameters to be determined parametrically (Beilharz and Mylrea 1963; Beilharz et al. 1966; Collis 1976). Kaiser's least squares method has also been used (Beilharz et al. 1966; Dickson et al. 1966). Regardless of the method of analysis, these values do have inherent faults and can give deceptive results. For example, an animal involved in relatively few interactions (< 5) may be given a deceptively high or low social rank because it interacted with a biased sample of opponents, a highly probable occurrence with such a small sample size. Therefore, care must be taken when interpreting hierarchies which have been constructed from such values.

In this study, the use of dominance values in constructing a hierarchy was necessary because of the limited number of pair combinations which were observed interacting. Beilharz's method of angular transformation was employed because of its relative ease and comparable performance to other methods (Beilharz et al. 1966). The major potential weakness of the ranking system was that the dominant-subordinate relationships between pairs of animals were often concluded from only one or two interactions. Repeated interactions possibly would have indicated a reversed relative rank in some cases. In addition, some animals from both hierarchies faced relatively few different opponents, making their estimated dominance values somewhat questionable. However, there is evidence to suggest that these weaknesses were not significant. For example, Beilharz and Mylrea (1963) found great similarities between hierarchies constructed from single and multiple days data and showed that dominance reversals occurred infrequently enough to enable hierarchies to be confidently determined from relatively few interactions. Secondly, the ewes with questionable dominance values in this study did not occupy unreasonable positions in the hierarchy, considering their opponents. Therefore, since the two hierarchies in this study reflected the dyadic dominant-subordinate relationships which had been observed, the correlation between various parameters to dominance could be assessed with some degree of confidence.

Younger herd members (< 2 years) were not monitored as intensively as the adult ewes and were excluded from the analysis of interaction data for this study. However, it did appear that from birth to early adult years, age and size (almost completely confounded factors during the growth period) were the predominant determinants of social status for female. In the study area, lambs were the most subordinate group of animals and appeared internally ranked by size, with the larger lambs usually initiating and dominating most encounters. Lambs did not assume the status of their dams at any time, a phenomenon observed in reindeer (Espmark 1964). The two female yearlings were the next most subordinate group, again clearly ranked relative to each other by size. As mentioned in Results, the three youngest adult ewes occupied the three lowest positions of the adult female hierarchy. Had suitable age estimates of the older ewes been available, a high correlation between age and dominance may have been evident.

The fact that weights and horn lengths were not consistently correlated to dominance during the study period likely resulted from certain statistically confounding factors. Animals in the 1977 herd which eventually died were invariably older ewes with longer than average adult horn lengths but with slightly reduced average weights because of their emaciated condition by early winter. Since their dominance position had been estimated primarily from the summer and early fall interactions before their physiological condition had deteriorated, there was little correlation between average weight and status by late fall and early winter, when weights were collected. Consequently, a low correlation coefficient between weight and dominance value resulted for the 1977 hierarchy. In 1978, with the absence of these moribund animals, weight proved to be significantly correlated with dominance.

The decreasing significance of horn length to dominance from 1977 to 1978 was more perplexing. Considering that several "long horned" animals of only intermediate status were removed from the herd in December, one would have expected the degree of correlation between horn length and dominance to show an increase from 1977 to 1978, and not the reverse. However, the promotion of two relatively short-horned individuals within the hierarchy in 1978 was sufficient to cause the correlation coefficient to drop to an insignificant level. This occurrence alone was possibly indicative of the borderline importance of horn length as a determinant of dominance in the captive ewes.

That aggressiveness and not physical attributes showed the greatest correlation to dominance is not surprising, considering the infrequency of physical interactions amongst ewes. Geist (1971) suggests that clashes between rams occur frequently enough to enable these animals to associate clash force with horn size. In such a system, large horns are an obvious dominance symbol. Among ewes, however, interactions are too infrequent and horn size differences are too subtle to allow an association between horn size and dominance status to develop. Consequently, particularly aggressive rather than large individuals could attain relatively high social ranks simply through intimidation. It was apparent that some ewes with new young became particularly aggressive, possibly explaining the rise in status of the two productive ewes. During actual

clashes and horn wrestling, weight becomes somewhat advantageous, which may explain this parameter's significance in the 1978 hierarchy. However, horn size, because of its limited variability in adult ewes, has little bearing on the outcome of such disputes and, consequently, is likely of little importance to rank.

Although these conclusions are based on limited data, they do appear similar to those from other social behaviour studies of female ungulate societies, where physical attributes show only minor differences between animals. Beilharz et al. (1966) and Collis (1976) both suggested that aggressiveness was the strongest predictor of dominance in cattle. Only Beilharz et al. (1966) showed weight to be an additional strong predictor while both authors reported insignificant and negative correlations respectively for height at withers and dominance. Schein and Fohrman (1955) showed age and weight to be significant indicators of dominance in cattle but further demonstrated that seniority in the herd, a factor confounded by age and weight, was the ultimate determinant of social rank. Dickson et al. (1966) found only weight to be significantly correlated to dominance. Espmark (1964) reported that age was of greatest importance in reindeer within a sex, while size and strength determined dominance between the sexes.

Chase (1973, 1974, cited in Wilson 1975) offers a "magnification process" hypothesis to explain the reason for the high correlation between dominance and aggressiveness. He suggests that aggressive individuals, by frequently initiating interactions with timid, submissive opponents, develop improved intimidating and fighting skills and become increasingly confident with each successful encounter. This increases the probability of success in later encounters, lifting the animal upward in the hierarchy until a social equilibrium is reached. Conversely, submissive animals eventually occupy low positions in the dominance order. "Accidental events, such as fatigue on a certain day or a chance blow" are suggested by Chase as reasons for the occasional dominance reversals which are observed in hierarchies.

CONSEQUENCES OF DOMINANCE

Diet Comparisons

The absence of differences in diet quality between the three social classes of ewes may simply have been a function of the distribution of their forage supply. During the winter months, the animals' diet was primarily fall regrowth from the study site's dominant grasses, a resource which was homogeneously distributed over the area (Wikeem, pers. comm.). Even when supplemental hay was provided, the herd still utilized native forage for much of the day. With such a dispersed food resource, there was little need for dominant animals to initiate costly aggressive disputes over feeding sites when equally good sites were readily available. Increased aggression did occur at the hay supply but most encounters were brief, enabling the initiator only to establish a feeding position. Probably the active exclusion of subordinates from the site would have been a needless and wasteful energy expenditure once the dominant animal had secured a feeding position. Consequently, time spent at the

supplemental feed did not vary between social classes of animals. Had the hay been contained within a feeder with a limited number of feeding spaces (e.g. 2 or 3), then dominance would likely have played a much greater role in resource allocation.

There is some indication that dominance in a group of animals competing for a limited point resource ensures an improved food supply to the high ranking individual. Wilson (1975) reports that the selection of anterior teats by piglets offers certain feeding advantages and that teat allotment may be dominance related. Espmark (1964) found that high social status in reindeer meant ready access to established feeding craters, but reported conflicting results on the advantages of dominant roe deer at supplemental feeding stations (1974a, 1974b). Some authors have even used a limited food supply to establish dominance relations between pairs of animals (Ross and Berg 1956).

An extensive literature search uncovered no reports which showed that dominance offers feeding advantages to animals exploiting a dispersed resource, similar to that found on the study site. A hypothesis presented in Geist (1974) suggests that the defense of such a thinly scattered resource by dominants incurs costly aggressive encounters without resulting in significant gain of resources. Geist further reasons that defense of abundant, localized resources such as supplimental hay is also energetically inefficient since effort would be better spent "feeding (increasing rate of food intake) rather than wasting time and resources fighting." Dominance during feeding is perhaps only beneficial to an animal when both feed and feeding spaces are limited.

Activity budget comparisons

In any detailed activity budget comparison, the method of data collection is of obvious importance to the accuracy of the eventual analysis. Scan sampling was the only available procedure suitable for such a large study site. It enabled data on a large number of group members to be collected simultaneously and readily provided data "appropriate to estimating percent of time spent in various activities" (Altmann 1974). The selection of a sampling interval was primarily dictated by the time required to collect information on the entire adult herd. A 15-minute interval, while occasionally excessive, was necessary for a complete scan when the animals were mobile, widely dispersed, or both. With such a lengthy time between scans, the percentage of intervals devoted to an activity can vary considerably from the actual percentage of time spent in that activity. However, this margin of error is most pronounced for short-term activities such as playing, nursing, etc., and was not considered significant for those of longer duration such as grazing and bedding. Data collected in this manner were sensitive enough to show significant day to day variations in the durations of the herd's major activity classes (grazing, bedding). Therefore, they were also considered valid for between-group comparisons of such activities.

A variety of scan sampling intervals have been used in the research of grazing behaviour but, unfortunately, no evaluation of the effects of

interval size within a given study has been made. Hancock (1954) used 1-, 2.5-, and 5-minute intervals at various times during his research on the grazing habits of dairy cattle. Van Dyke (1978) maintained a five minute interval throughout his study on the activity budgets of bighorns in Oregon. The majority of studies dealing with large areas and group sizes have used a 15-minute sampling period for data collection (reindeer, Thompson 1971; caribou, Roby 1978).

The hypothesis proposed for this section predicted that dominant animals, by having access to higher quality foraging areas, would have reduced feeding times from subordinate herd members. However, the study animals were exploiting a relatively dispersed food resource where social status meant little to the acquisition of food (see previous section on diet comparisons). Since the animals were able to express their own foraging selectivity with minimum interference from other herd members, it would follow that the average grazing times of the three social classes would not vary significantly. This proved to be the case.

The degree of within-class variability in the grazing and bedding times of the three social classes suggested the effects of various biological factors on the foraging behaviour of animals. Throughout the fall and winter months, the subordinate animals differed significantly from each other in their activity patterns in only two of the seven months tested. From September to December, the dissimilar grazing or bedding times of intermediate animals added significant variance to the statistical model in every month. However, after the winter deaths, their activity budgets showed significant within-class variation only in January. Dominant animals showed significant within-class variability in more months than the subordinates but in fewer months than intermediates. The group size and the degree of within-class variation appeared to vary directly. However, certain biologically influenced trends also became evident when the composition of each group is considered. The subordinate group was comprised of an age cohort and contained no members with a detectable, aberrant physiological condition. The dominant group likely had a wide age range and, from October to December, contained one sick animal (high SGOT) which eventually died. The intermediate group also likely contained a wide age range and, from October to December, five animals with elevated SGOT levels, four of which died in winter. Therefore, it is possible that age and physiological condition were at least partially responsible for the variable behaviour of herd members. A more detailed discussion on the effects of physiological condition on grazing behaviour is presented later.

Studies on domestic herbivores have shown the effects of age on grazing behaviour. Hancock (1954) found little variability in the behaviour of twin heifers under identical environmental conditions, indicating the possible importance of genetic as well as age factors on the behaviour of animals. Although he did find variable behaviour between unrelated sets of similar aged twins, he attributed these differences to different levels of milk production amongst the sets. Arnold and Maller (1977) found that animals with greater periods of foraging experience in a given environment take longer to adapt to new grazing

regimes than animals of limited previous experience, a plausible explanation of why age can affect grazing behaviour. In light of captive animals in this study, the dominant and intermediate ewes, having variable ages as well as variable foraging experience, each adopted a slightly different foraging pattern while adjusting to the new vegetation, resulting in significant behavioural differences. The subordinates, because of young age and limited previous experience, were quick to develop a common appropriate foraging strategy for the study site. This argument became more convincing when behavioural data on lambs born on the study site and yearlings were assessed. The three yearlings in the herd, with less than one year of previous foraging experience on native range, showed no significant within-group behavioural variation in any of the months tested. Similarly, lambs born and weaned on the study site, demonstrated remarkably low within-group variability in activity budgets once separated by sex.

Productivity comparisons

The lack of between-class production differences can logically be attributed to the similar diets of the three social classes. Without obtaining a higher quality forage supply than other animals, dominant ewes would not be expected to demonstrate greater productivity. Certain between-class trends in production, although statistically insignificant, did seem apparent but most could be interpreted in terms of factors other than social status. For example, the average weight gain of Subordinates from March to August which appeared high compared to that of Intermediates and Dominants was likely the result of growth as well as seasonal weight fluctuations. A review by Shackleton and Shank (in press) showed both Rocky Mountain and California bighorn ewes continue to grow after three years of age. Similarly, Geist (1971) suggested that bighorn rams approach their maximum weight at 5 - 8 years of age. Therefore, it is probable that the subordinate ewes of this study, all three years of age, were still demonstrating some physical maturation which contributed to their March to August weight increase. This, of course, was not the case for the older animals of the remaining two social classes. The fact that all three subordinates were, on average, 5.0 kg heavier in August 1978 than in September 1977 supports this suggestion.

The apparent, although statistically insignificant, preponderance of winter mortalities within the intermediate social class can possibly be attributed to age rather than social status. As described in Results, animals which died were invariably older individuals (6+) with considerable gum necrosis and tooth loss, a condition which affects the prehension, mastication, and even digestion of forage. Age alone enabled these animals to dominate the young subordinates in the herd. However, because of their relatively poor physical condition for much of the year, these animals, with the exception of the dominant ewe WWW, were unable to express the aggressiveness necessary to achieve high ranking status. (Even WWW, although dominant, was relatively docile, initiating only a moderate number of interactions compared to other dominant animals). Consequently, the majority of deaths occurred within the intermediate social class.

Few studies of female ungulate societies have fully investigated the relationship between dominance and productivity. An extensive literature review found no research which assessed the effects of dominance on offspring production, even though a positive correlation between these two factors has been suggested for the males of many ungulate species (mountain sheep, Geist 1971; pronghorn, Kitchen 1974). Similarly, attempts to compare other measures of the productivity of dominants and subordinates such as their seasonal weight fluctuations and their offsprings' growth and behaviour have not been reported.

Since such production comparisons require long-term observations of animals in a captive state, it is not surprising that such research has concentrated on domestic animals. In research on dairy cows, Schein and Fohrman (1955), Beilharz et al. (1966), and Collis (1976) all found no relationship between dominance and milk production. In addition, Collis (1976) found that levels of certain blood constituents, considered indicative of nutritional status, were not correlated to dominance. He suggested that "it was unlikely that dominant animals had a greater rate of production than subordinate animals....., primarily because of..... the system of management on the farm, which nullified any possible nutritional advantage for dominant individuals....." In a similar fashion, the homogeneously dispersed nature of the forage on our study site prevented dominants from obtaining any nutritional advantages and, consequently, from demonstrating greater productivity than subordinate animals.

FORAGE AVAILABILITY AND HERD BEHAVIOUR

Unlike the investigation of the captive herd's social organization, which enabled certain hypotheses to be accepted or rejected based on statistical procedures, research on the herd's seasonal diurnal behaviour was not oriented towards statistical analysis, hypothesis testing, and inductive reasoning. Instead, causal factors for behavioural trends could only be hypothesized (i.e. retroduction, Romesburg 1981). Although alternative hypotheses could have been generated from the same information collected during this study, those presented below offer the strongest interpretation of the animals' behaviour.

Seasonal diurnal patterns

Seasonal changes in the diurnal pattern of the captive herd likely resulted from a complex interaction of abiotic and biotic environmental variables, a concept expressed by most researchers of herbivore behaviour (Arnold and Dudzinski 1978). Abiotic factors can easily be related to certain changes in the herd's behaviour. For example, although these animals showed some nocturnal tendencies, the onset and termination of their diurnal routine generally centred around dawn and dusk, respectively. Consequently, the time of sunrise and sunset (i.e. daylength) influenced the timing of two of the animals' major active periods, early morning and late evening. Similar findings have been reported in other bighorn studies (Mills 1937; Davis 1938; Davis and Taylor 1939; Blood 1963; Geist 1971; Van Dyke 1978) and from studies of domestic livestock

(Hughes and Reid 1951; Hancock 1954; Sheppard et al. 1957; Arnold and Dudzinski 1978). Although not statistically assessed, daylength also proved to be inversely related to the number of active and non-active periods demonstrated by the herd during the daylight hours, a trend also reported from other relevant studies. Arnold and Dudzinski (1978) stated that "...in latitudes greater than 35° the breaks between grazing decrease, as the days get shorter, until in mid-winter some animals will always be found grazing during daylight."

Although detailed weather information was not available for the study site, it appeared, from direct observation, that daily weather patterns had only minor temporary effects on the herd's behaviour. For example, cold inclement conditions in December were likely responsible for the herd's reduced early morning activity, a behavioural pattern also reported for Stone's sheep (Geist 1971). Domestic livestock (Arnold and Dudzinski 1978) and deer (Severinghaus and Cheatum 1956, cited in Moen 1973) also demonstrate reduced activity during particularly cold days or cold portions of a day. Severe rain storms in the summer also appeared to affect the herd's behaviour temporarily, frequently eliciting a brief but often premature bedding period by the herd. Similar behaviour has also been reported in domestic livestock (Arnold and Dudzinski 1978).

In spite of their apparent influence on behaviour, the combined effects of both weather and daylength could not fully explain the broad seasonal changes in herd behaviour. For example, data from April and September, months of comparable temperatures, precipitation, and daylength, demonstrated vastly different average activity patterns and budgets for the herd, suggesting that other factors must play a major role in influencing herd behaviour.

Based on information provided from Wikeem's (pers. comm.) research and from other relevant grazing studies, forage availability and phenology were likely the factors most influential in shaping the seasonal diurnal patterns of the herd. Although it was a direct consequence of both daylength and general weather patterns, forage condition, in all probability, more directly dictated the required foraging effort and subsequent behaviour of the herd.

Certain recognized relationships exist between an animal's foraging behaviour and forage quality and quantity. It is widely reported that grazing animals are highly selective for both specific plants and specific plant parts. Arnold and Dudzinski (1978) summarized that from the single plant, sheep and cattle eat leaf in preference to stem, green (or young) material in preference to dry (or old).

The degree of selectivity expressed by an animal is often closely related to intake rates. Arnold and Dudzinski (1978) stated that for sheep, intake rates were related to "...yields per unit area of green and dry pasture, length of pasture, number of leaves per unit area and diet digestibility." Generally, as forage matures, herbivores are particularly selective for new rather than old growth (Meyer et al. 1957; Arnold 1960b) and thus, selectivity is often to the detriment of intake rates (Arnold and Dudzinski 1978).

In slightly more detail, White and Trudell (1980) summarized the extrinsic factors limiting forage intake rates in caribou and reindeer as being:

a) food availability - biomass
- protection by snow
- protection by dead plant material

b) food quality - low dry matter digestibility due to fibrousness
- low dry matter digestibilities due to digestive inhibitors (e.g. tannins)
- toxic plant compounds

c) harassment - by insects and predation

d) behavioural interactions during - calving
- rutting
- resource competition.

That grazing times generally increase with decreasing pasture quality and decreasing intake rates has been documented by a much larger number of researchers. Allden and Whittaker (1970) stated that "when accessibility of herbage imposed limitations on the rate at which the animal was able to prehend its feed, it was shown that the sheep was able partially to compensate for the reduced amount of herbage present by an increase in grazing time (from 6 to 13 h/day)." Similarly, Arnold (1960; sheep), Hancock (1954; dairy cattle), Sheppard et al. (1957; beef cattle), and Waite et al. (1951; dairy cattle) all reported an increase in grazing time for animals with decreasing forage quantity, quality, and/or palatability. Such trends generally meant longer but less frequent foraging bouts with declining pasture conditions. As previously discussed, Arnold and Dudzinski (1978) reported the increasing duration of grazing bouts with decreasing daylength, a trend likely associated with declining pasture conditions more so than daylength.

Some studies on other species have shown similar seasonal diurnal trends. For example, Thompson (1971) showed that activity periods of wild reindeer decreased in length and increased in frequency from winter to spring months, although he presents no interpretation for this trend. Reporting similar results for the central Arctic caribou herd, Roby (1978) suggested that increased forage availability in the summer months "... reduces the time required to fill the rumen and increased quality would be expected to reduce rumen turnover times."

Based on the above relationships, a detailed interpretation of changes in the herd's seasonal diurnal patterns has been developed. It is postulated that the change from the cyclic nature (i.e. successive intervals of feeding and bedding) of the herd's activity pattern in spring and summer to the more continuous foraging behaviour of the fall was closely related to declining forage conditions. As discussed in Results, many preferred dietary species of grasses, shrubs, and forbs were abundant in the spring and summer and in a rapid growth phase. In addition, the continuous foraging behaviour of the fall was closely related to declining forage conditions. As discussed in Results, many preferred dietary species of forbs (e.g. Balsamoriza sagittata and Lupinus sericeus) were relatively large and succulent and the tiller lengths of utilized grasses were relatively long, a condition conducive to large bite sizes in the grazing

animal (Allden and Whittaker 1970). Since forage in this phenological state has been shown to be high in crude protein and highly digestible (Hebert 1973), the captive animals likely had rapid intake and assimilation rates, in spite of the high degree of species selectivity which they demonstrated during the period (Pitt and Wikeem 1979). Considering that the rate of passage of ingesta varies directly with its intake rate and digestibility (Blaxter et al. 1961), the turnover rate for the ingested forage was probably high. This rapid turnover rate would enable the sheep to fill their rumens and then ruminate several times during daylight, in the cyclic fashion demonstrated.

The change from this cyclic pattern of successive feeding and bedding-ruminating periods to the more continuous foraging behaviour in the fall partially resulted from the increasingly dispersed distribution of the captive herd and the asynchrony of separate subgroups. That is, different subgroups frequently out of visual range of each other, began to bed and forage at slightly different times, causing activity graphs for the herd as a whole to fluctuate less drastically, and to indicate a relatively constant, high level of activity throughout the day. However, analysis of individual animal activity patterns demonstrated that animals were, in fact, foraging more continuously as the fall months progressed and that the herd activity graphs were not misrepresenting the herd's true behaviour. This gradual conversion to continuous daylight activity seemed to coincide with the late season maturation and fall regrowth of the study site's vegetation. The declining availability of forage from shrubs and ephemeral forbs preferred by the herd during the spring and summer appeared to force the animals to utilize the more common grass species of the study site (Wikeem, pers. comm.). However, this regrowth, often shrouded by less palatable, apical plant parts, was not as accessible or as abundant as preferred forage in previous months and likely required a considerable degree of foraging effort to procure it. It is postulated that the time required to express this selectivity and a reduction in bite size reduced intake rates, enabling the animals to forage throughout most of the day without repeatedly filling their rumens and without frequent bedding-ruminating periods. It is further suggested that this trend became increasingly more pronounced during the fall months because regrowth became less available and intake rates further declined.

The absence of high levels of activity throughout the day during the inclement period of December appeared, in part, to be the consequence of low temperatures, as previously discussed. However, the bedding period at mid-day, when temperatures approached the daily maximum, may have reflected a need to ruminate. It is unlikely that an increase in intake rates prompted the rumination period, considering the snow accumulation at that time. However, it is possible that a decrease in the digestibility of the forage consumed by the herd may have been a factor. The deep snow covered any remaining regrowth and the sheep, although cratering to some extent, seemed content to feed largely on stems and seed heads of bluebunch wheatgrass and on browse species which were above the snow. This high fibre forage, being less digestible and slowly processed, would have forced the herd to bed and ruminate after short foraging periods. Hoefs (1974) offered a similar explanation for the mid-day "siesta" observed in his captive Dall's sheep herd.

Once the snow cover disappeared from the study site, the sheep reverted back to a more continuous foraging behaviour. The animals were observed feeding low to the ground, possibly selecting the most recent growth of the plants once again. It is postulated that, similar to late fall foraging conditions, intakes rates were sufficiently low to enable the animals to forage continuously throughout the daylight hours without resting to ruminate.

The activity patterns demonstrated by the herd in January were naturally influenced by the presence of supplemental feed. From dawn to late morning, most, if not all, of the captive animals were concentrated in the vicinity of this feed. By foraging at such an easily exploited, point food resource, each animal could fill its rumen and process the ingesta relatively quickly, enabling the animal to feed and ruminate two or three times before the hay was depleted. Because the herd members were not synchronous in their activities around the feed supplement, likely because of the limited foraging space, the activity graph (Fig. 1) indicates an avoidance of the early morning hours by the animals for January. Such behaviour was not apparent, as it was during the inclement cold weather period of December, probably because of the easy and energetically efficient foraging conditions afforded by the hay pile.

Since hay was provided at a rate of only 45 kg/day, this supplemental food source was depleted by late morning. Consequently, the animals were forced to utilize the study area's native vegetation during the afternoon. Clumps of vegetation on the lower half of the enclosure were snow free for much of late January and the animals restricted their foraging to these areas. By primarily selecting the fall regrowth at the base of the more common grass species (Agropyron spicatum, Koeleria cristata) (pers. obs.; Wikeem, pers. comm.), it is postulated that the animals again had sufficiently low intake rates to reduce the rate of rumen fill and, consequently, eliminate the need for inactive ruminating periods. As a result, the majority of the animals did not bed until nightfall, when temperatures again began to drop.

In February, warmer mean-daily temperatures and the loss of snow from the study site's lower elevations provided the animals with similar foraging conditions to those experienced in November and the mild periods in December. Still selecting the fall regrowth of the study site's common grasses, the herd not surprisingly demonstrated similar daily activity patterns to those months.

During March, the new growth of spring offered a highly nutritious food source to the animals. However, in its initial development, this growth was not abundant, being homogeneously but lightly dispersed over the lower half of the study site. In the grasses and forbs, growth occurred low to the ground and, similar to fall regrowth, was often shrouded by less palatable, cured plant parts or litter. As previously discussed, the animals selected this new growth (Wikeem, pers. comm.) and demonstrated a more cyclic and synchronous pattern of feeding and bedding-ruminating periods than in previous fall and winter months. It is postulated that the new growth enabled the animals to increase their forage intake and assimilation rates, resulting in the return of the herd's cyclic activity pattern which predominated in the spring and

summer. Activity peaks were, however, longer and less frequent than in the spring and summer months, suggesting that the low density spring growth was sufficiently dispersed or inaccessible to keep intake rates below maximum levels.

The additional activity data collected in November and December, 1978, although limited in quantity, further demonstrated the effects of forage quality and quantity on the herd's diurnal behaviour. On November 14, 1978, the herd, under seasonable weather conditions, demonstrated a cyclic, synchronous activity pattern of successive feeding and bedding-ruminating periods. Other researchers observing the herd during November reported similar behaviour for the herd (D. Eastman, A. Bottrell, pers. comm.). This pattern was completely unlike the more continuous activity levels observed in November, 1977 and appeared to be related to forage condition on the study site. The summer and fall months of 1978 were relatively wet for the Okanagan region and, consequently, many of the enclosure's major plant species remained in a high quality, vegetative state until the colder, drier weather of October (Wikeem, pers. comm.). It is postulated that this unusually productive growing season, coupled with a vastly reduced herd size in 1978 (40% reduction), resulted in large quantities of highly nutritious, readily accessible forage being available even in November (Wikeem, pers. comm.), allowing the animals to repeatedly fill their rumens and ruminate in a cyclic fashion more typical of spring and summer periods.

On December 17, 1978, green fall regrowth was still available to the animals but was covered by a 15 cm cover of powder snow. Unlike their behaviour during similar foraging conditions in early December, 1977, the sheep did not appear to utilize seed heads and browse species protruding above the snow but chose instead to crater to the regrowth. Their selection of this energetically more costly foraging strategy was possibly a reflection of their improved physiological condition over that of December, 1977 or the greater abundance of fall regrowth or both. Their cratering efforts possibly slowed intake rates sufficiently to allow the animals to forage in a continuous fashion throughout the day, unlike the comparable period in December, 1977 when a mid-day bedding-rumination period was required.

Several studies have presented data on the activity patterns of mountain sheep but few make detailed seasonal comparisons or interpretations. During the spring and summer months, most bighorn populations showed fewer activity peaks than our captive herd, although active periods at dawn and late afternoon, as previously discussed, were invariably present. Mills (1937) and Davis (1938) both found three peaks of activity for a Yellowstone National Park population, occurring at dawn, mid-day and in the late afternoon. Davis and Taylor (1939) found a bimodal activity pattern in Texas bighorns with foraging peaks extending throughout the morning and late afternoon. A single rest period occurred at mid-day. Van Dyke (1978) found early morning and late afternoon to be the only consistent periods of activity for Oregon bighorns.

Reports on the fall activity patterns of wild sheep more closely resemble 1978 rather than 1977 data for the captive herd. Geist (1971)

found an average of four activity peaks for Stone's sheep rams in October, with one major bedding period at mid-day which involved almost all visible animals. Hoefs (1974) found that a captive Dall's sheep ram also demonstrated a mid-day bedding period during the fall (except during the rut), with three or four active periods during daylight. Van Dyke (1978) again noticed only early morning and late evening activity peaks, with an extensive mid-day resting period. Researchers have reported variable activity pattern for wild sheep herds during winter months. Similar to the inclement weather period of this study, Geist (1971) noted that Stone's sheep fed little in the morning, with an activity peak occurring at noon and again in late afternoon. Blood (1963) presented similar results for California bighorns but showed a third activity peak at dusk. However, Hoefs (1974) and Van Dyke (1978) found no avoidance of the morning hours by mountain sheep in their studies. Instead, sheep showed a major activity peak in early morning and late afternoon, with an extensive mid-day rest period.

Since results from this study have indicated the importance of forage quality to the diurnal behaviour of sheep, the between-site discrepancies discussed above are difficult to interpret without more detailed range information on each site. The relatively large number of activity peaks demonstrated by our captive herd in spring and summer, for example, may simply reflect a more concentrated, readily available food resource on the study site than on other, natural ranges, allowing for more rapid rumen fill. Differences in the size of study areas may have also caused the discrepancies between this and other studies. Animals occupying a larger, more rugged natural range likely showed less synchrony within a herd than did our captive sheep. This asynchrony would have obscured the more multi-peaked activity pattern of individuals, particularly without animals equipped with identity collars.

Nocturnal activity

Although limited activity data were collected during the hours of darkness, certain characteristics of nocturnal behaviour were apparent and seemed to be of practical and bioenergetic significance. As previously discussed in Results, night foraging bouts were not as frequent nor as lengthy as those during daylight hours. They usually involved less than 50% of the herd at any one time and were restricted to the immediate vicinity of the bedding area. This behaviour may have some survival value. Although sheep obviously possess relatively good night vision, it is likely not as developed as that of some nocturnal predators. By limiting their foraging bouts to areas near other feeding or bedding animals, sheep reduced the risk of being singled out and attacked by a predator. It would appear that sheep have also modified their diurnal patterns to ensure minimal night activity. Almost invariably, sheep demonstrate their most extensive foraging period late in the day, in the spring to fall period of the year. This may function to fill their rumens to their greatest capacity of the daylight period, without the thermal discomfort that would occur during the hotter portions of the day. Such a strategy would, in turn, reduce the stimulus to forage during the night.

The apparent decrease in nocturnal activity by the sheep during the colder winter months was likely an energy conserving strategy, consistent with their avoidance of early morning hours. Foraging in thermally and visually suboptimal conditions probably results in a greater negative energy balance than simply bedding and conserving heat, particularly if good visibility is required by sheep for efficient forage selection.

Other authors have reported on the nocturnal behaviour of mountain sheep but in little detail. Geist (1971) reported that sheep are active and widely dispersed at nightfall, with sufficiently developed night vision to enable them to retire to rugged cliff terrain during darkness. Woolf et al. (1970) noticed feeding at intervals throughout the night but suggested that movements were "limited to the immediate vicinity of the bedground." Van Dyke (1978) also reported some night movements in bighorns.

A further discussion on the possible seasonal trends in the nocturnal behaviour of the captive herd appears in a later section.

Seasonal activity budgets

As previously discussed, research on domestic animals has shown an inverse relationship between pasture quality and grazing times (Sheppard et al. 1957; Arnold 1960a). Such a trend was not obvious for the captive herd from their daily activity budgets. Although the animals devoted a greater proportion of the day to foraging as pasture conditions declined, they were simply unable to increase their daylight foraging times substantially because of shortening daylengths. Research has shown that bighorns maintain relatively high total intake levels over a 24 h period during the early fall months (Hebert 1973; Chappel 1978), at least until crude protein levels drop below 7 to 8% (Hebert 1973). Considering that Wikeem (pers. comm.) found crude protein levels of the fall regrowth of utilized grasses to exceed this value easily, it appears that the captive herd was attempting to maintain relatively high nutrient intake levels, likely as a prewintering fattening requirement. However, with the proposed reduced intake rates for this period of the year, it is doubtful that the diurnal grazing times of the herd were sufficient to provide adequate nutritional levels. Consequently, it is hypothesized that the herd increased its nocturnal grazing times as daylength decreased, and that total grazing time for the herd over a 24 h period peaked in the early fall. A secondary peak may also have occurred in spring with the onset of body growth and, to a secondary degree, reproductive demands. Arnold and Dudzinski (1978) noted such a trend of increasing nocturnal activity for cattle and suggested that .."the proportion of night grazing was significantly related to total grazing time (+ ve), daylength (- ve) and latitude (- ve), with daylength being the most important." A similar relationship appears to exist for domestic sheep (Arnold and Dudzinski 1978, Fig. 1.2).

Based on the diurnal and limited nocturnal data collected on the study animals during December and January, this trend of increasing foraging times for the complete 24 h period with decreasing daylight was disrupted during the winter months, when the herd reduced their foraging

times and efforts considerably. Such reduced winter activity in bighorns, reportedly an energy conserving strategy, has been suggested by Geist (1971) and Chappel (1978) and is associated with reduced metabolic and intake rates (Chappel 1978). Since Arnold and Dudzinski (1978) reported that supplemental feed generally reduced the grazing time of pasture animals, January's low foraging value was probably the result of both the supplement food source and the reduced winter activity suggested above. Reduced nocturnal activity during the winter has also been documented, although not specifically for bighorns. Ozoga and Verme (1970), in studies on penned white-tailed deer, reported two nocturnal activity peaks in early winter, but a decline in night activity as the winter progressed. Craighead et al. (1973) found that elk "actually bed more per hour of darkness during the winter than summer", with animals spending ..."most of the hours of the long winter night bedded...."

Both observed and suggested trends for the herd's daily grazing efforts and times have been reported by other researchers of wild ungulates. Van Dyke (1978) found bighorn daylight foraging effort (i.e. proportion of daylength) to increase from summer to winter. He attributed this trend to:

a) less daylight available in which to be active in winter;
b) poorer forage quality in winter;
c) less available forage in winter;
d) colder temperatures in winter which cause an increase in energy demands.

(In light of Chappel's (1978) findings on the thermal neutral zone of bighorns, this last postulation seems questionable).

Craighead et al. (1973), in their study of radio-collared elk in Yellowstone National Park, found total feeding times over 24 h peaked in fall and spring, with considerably reduced times being evident in summer and particularly in winter.

Within the reduced winter activity regime of the study animals, the degree of winter foraging effort on a daily basis seemed largely dependent on the accessibility of forage. The captive herd, as previously discussed, devoted considerably more daylight time to foraging during the mild, snow-free period of late December, 1977 than during the more difficult foraging period of early December, 1977, when ground accumulations of snow reached 30 cm. Similarly, Craighead et al. (1973) attributed low foraging times in winter to a "scarcity of palatable food, travel restrictions imposed by deep snow, and the need to conserve energy." Roby (1978) offered an opposing view on the impacts of snow cover, suggesting that foraging efforts were greatest when snow depths and cratering requirements were greatest.

Since the captive sheep generally ruminated in a prone position, bedding times for the herd were largely a function of the herd's rumination requirements. Consequently, bedding times were strongly correlated to daylength, peaking in the spring and early summer when forage intake rates were presumably high and dropping in the early spring

and fall when intake rates were presumably lower and foraging effort high. The mid-winter peak, less pronounced than in spring and summer, was likely the result of the herd's reduced activity levels, rather than higher intake rates. It can be speculated that, over a 24 h period, total bedding times would likely have been higher in winter than at any other time of the year because of the limited nocturnal activity during the long winter night.

Similar to this study, Van Dyke (1978) generally found diurnal bedding effort to be the reciprocal of feeding effort. Craighead et al. (1973) found bedding times over a 24 h period to be relatively consistent in spring, summer, and fall, and high in winter.

A detailed interpretation of the seasonal fluctuations in times devoted to the other behavioural categories is of limited value. A 15-minute sampling interval proved to be too long to provide accurate activity budget data on such short-term events as standing, travelling (walking, running), and "other" activities (nursing, interacting, playing). However, certain seasonal trends in such behavioural categories were apparent and can be discussed. For example, the relatively high proportion of time devoted to standing during the coldest months appeared to reflect a behavioural adaptation of the animals to low temperatures. Both Geist (1971) and Chappel (1978) reported that bighorns frequently stood in a "closed standing posture" (Chappel 1978) to combat cold temperatures, rather than bed. It can be speculated that such a posture offers equivalent or greater energy conservation than bedding, in certain circumstances. Generally, preferred winter bed sites for the captive herd occurred under large Ponderosa pines (Pinus ponderosa), where accumulated litter was available as an insulating bedding material and where the tree canopy likely reduced heat losses to long wave radiation. However, in December, January, and February, foraging was largely confined to the supplemental feed or the lower third of the study site, where only three preferred bed sites occurred. Consequently, on many occasions, animals requiring a period of rumination were a considerable distance from one of these sites. Rather than travel to such a site or bed on uninsulated ground during the active period of the day, animals frequently chose to stand. (Major treks to and from the preferred bed sites did occur at dawn, dusk, and, occasionally, at mid-day). It is possible that convective heat losses in such a position constituted less of an energy drain for short periods than walking to preferred sites or bedding on uninsulated ground.

The relatively high proportion of time devoted to travel in April reflected a general high level of "flighty" behaviour for the herd in that month. The herd frequently made long treks between foraging bouts and "panic" flights for no apparent reason. This behaviour continued into May, although at reduced levels, during the early development of that year's lambs. Difficult to interpret, such flighty behaviour seemed to occur simultaneously with the return of optimal foraging conditions, indicating a possible relationship to increasing available energy. The presence of lambs with their highly energized play bouts seemed to prompt such behaviour to continue throughout May. The high travel proportions in December appeared to result from the opposing distributions of feeding

and bedding sites. Animals almost invariably chose areas adjacent to the water paddock for major bedding periods, while preferred feeding sites of reduced snow accumulations occurred more than 0.5 km to the south. This resulted in relatively frequent observations of travelling animals, particularly in the morning and late evening.

The relatively high proportion of daylight times devoted to "other" activities by the herd appeared related to the maternal interactions between ewes and their lambs. Nursing, which peaked in May and early June, was the predominant contributor to this activity category. Interactions and play bouts amongst the ewes, but generally initiated by the lambs, consumed the remaining time devoted to this category. That rutting activities did not produce a secondary "other" activity peak in November accurately reflected the quiescent rutting period of the herd. It appeared that few ewes became sexually receptive in 1977, either because of their poor physiological condition or the inexperience of the young rams introduced for the rut. Other studies using similar scan sampling techniques to this one have reported on a fall peak in "other" activities, generally related to the rut (Roby 1978; Van Dyke 1978).

Daily variability in herd behaviour

As previously discussed in Results, the day to day variability in the herd's behaviour was a significant source of variation in the linear model used to analyze herd behaviour in all months but January. With the exception of data collected in December, there was no evidence to suggest that such variability was the result of gross weather patterns (i.e. mean daily temperatures, daily maximum and minimum temperatures, precipitation). However, more subtle weather factors such as changes in barometric pressure, wind speed, and relative humidity have been linked to changes in animal behaviour (Arnold and Dudzinski 1978) and, in all probability, were at least partially responsible for daily behavioural variation in the captive herd. Further work in this area is required to validate such a suggestion.

Day to day changes in behaviour have been documented for domestic grazers. Hancock (1954) reported that day to day differences in the grazing and ruminating times of dairy cattle accounted for 50 and 60% of the total variation in times devoted to these activities. Hancock attributed these daily variations to fluctuations in weather and range condition. Sheppard et al. (1957) also found grazing times between days to vary significantly for cattle, but much less so for consecutive days. They suggested that "climatic or light factors" and "pastures and other biotic factors", all of which influence grazing behaviour, "are more nearly alike on consecutive than on non-consecutive days ...." January's data from this study supports Sheppard's suggestion. January's sampling days, unlike those of other months, were consecutive and behavioural data, as previously mentioned, showed no day to day variation.

EFFECTS OF PHYSIOLOGICAL CONDITION ON DAILY ACTIVITY BUDGETS

An aberrant physiological condition such as malnutrition appeared to affect the captive herd's diurnal pattern more grossly than normal pregnancy. The increased grazing times of sick animals in October may have been an early attempt to improve their condition before winter. In December, with declining health and low fat reserves, these animals appeared to convert to an energy conserving strategy even more pronounced than the remainder of the herd. While maintaining a foraging effort equivalent to other herd members, the ailing animals bedded longer and reduced energetically costly activities such as travel and social interactions.

This observed behavioural trend seemed consistent with the limited literature available. Arnold and Dudzinski (1978) generalized that "thin sheep eat more than fat sheep under all pasture conditions" by grazing longer and usually eating faster than fat sheep. However, under extreme weather conditions (i.e. cold), a reversed trend was noted, with sheep in poor condition reducing grazing times (Arnold and Dudzinski 1978). Similarly, Roby (1978) found that a caribou herd from a poor winter range in Greenland and suffering from high winter starvation rates demonstrated higher bedding times than a better nourished caribou herd in Alaska. Moen (1973) suggested that a deer employing several energy conserving strategies, including bedding with its head down, could reduce energy losses to 2 x BMR even in -40°C weather. Such a strategy would be of obvious importance to an ailing animal during difficult foraging conditions.

The fact that pregnant ewes in the herd demonstrated no greater foraging times late in pregnancy than did barren ewes is also consistent with the literature (Arnold 1962; Arnold and Dudzinski 1978). While it is generally accepted that pregnant ewes have increased nutritional demands during final stages of fetal development, it appears that these increased demands are not extensive (Blaxter 1962) and are possibly met by an increase in rate of eating, rather than an increase in grazing time (Arnold 1962). Such a response is particularly possible during late stages of pregnancy when forage quality and quantity is generally high and the forage is easily harvested.

ENERGY EXPENDITURE ESTIMATES FOR THE HERD

The average BMR's estimated for the herd members using Chappel's (1978) predictive model ranged from 2.75 kcal $kgW^{-0.73}/h$ in July-August to 4.79 kcal $kgW^{-0.73}/h$ in June. These values were generally higher than Brody's average figure for mammals of 2.94 kcal $kgW^{-0.73}/h$ (Blaxter 1962). It would appear that my estimated bighorn BMR's were also higher than that for domestic sheep. Both Marston (1948, cited in Blaxter 1962) and Ritzman and Benedict (1930, cited in Blaxter 1962) found FMR's of only 2.46 kcal $kgW^{-0.73}/h$ for adult merino ewes. However, neither the elevated values of our captive bighorns nor the monthly variability of these values seem unreasonable, since BMR's (and FMR's) have been

demonstrated by other researchers to be both species specific and highly variable within species. For example, Blaxter (1962, Table 17) showed that the FMR's of steers estimated from various studies ranged from 3.33 to 4.01 kcal $kg^{-0.73}/h$. In addition, Ritzman and Benedict (1938, cited in Blaxter 1962) ...."found metabolism to vary in the same individual by 40% or more, and they showed that much of this variation appeared to be associated with the time of year, maximum values being obtained in the spring and early summer."

The irregular seasonal fluctuations in the BMR's developed for the captive herd only slightly resembled trends reported by other researchers. Chappel(1978) found spring and particularly fall FMR values to be noticeably higher than winter values. Chappel also found forage intake rates of his study animals to be higher in spring and fall than in winter, as did Hebert (1973). A similar seasonal trend has been recognized for several wild, high latitude cervids (white-tailed deer, Silver et al. 1969, 1971; caribou and reindeer, McEwan and Whitehead 1970). It has been suggested that the reduced winter rates reflect a winter "growth dormancy" period (Reimers 1980) which enables the animals to best cope with low winter temperatures and food shortages. The generally higher spring to fall rates, in turn, coincide with "...the increased energy requirements in this season due to rapid growth, lactation, moulting, antler growth and increased activity" (Reimers 1980). Although the typical spring - early summer peak and late winter low in BMR values were estimated for the captive herd, late summer - fall BMR's were unusually low, compared to trends discussed above. Their low value may have been an artifact of Chappel's predictive model, since seasonal correction factors for the June to September period were extrapolated values and not based on actual FMR readings from his study animals. However, Chappel's data do indicate that high ambient temperatures ($> 10^{\circ}C$) have a depressive effect on metabolism. From this information, one could speculate that bighorns may lower their metabolic rates following peak reproductive and growth demands and prior to rutting and pre-wintering periods to combat excessive heat loading during the hot summer period. Blaxter (1962) discussed the potential for such heat loading, in poorly insulated domestic animals exposed to extensive, direct solar radiation. However, bighorn researchers have not reported on a late summer reduction in forage intake by these animals (Hebert 1973), a condition which would likely arise with reduced metabolic rates. Similarly, behavioural studies (Kornet 1978; Van Dyke 1978; this study) have shown little or no avoidance of the hottest portion of the day by bighorns, a behavioural pattern which should have been evident if heat loading was a problem. Until further work on late summer bighorn metabolism is completed, little can be said on this aspect of their biology.

Activity costs estimated for the herd on a monthly basis were significantly correlated to monthly BMR's ($r^2 = .93$, $p < 0.05$), in spite of activity budget changes over the year. One might conclude from this information that the captive herd did not rely on seasonal behavioural adaptions to modify their energy expenditures, since the expenditures of the animals were predominantly controlled by physiological adjustments to BMR. While this may largely be true, it can be demonstrated that behavioural adaptions may have been important in determining the herd's

net energy balance. In general, relatively "expensive" activities (walking, running, "other") which offered no direct energetic returns comprised a decreasing proportion of the herd's energy expenditures from spring (April) to late winter (March), with proportions declining from 30 to 11%, respectively. (Because of high travel times in December, interpreted in the previous section, this trend was disrupted slightly in mid-winter). Conversely, relatively "inexpensive" yet essential activities (grazing, bedding-ruminating) which yielded gross energetic returns (i.e. assimilated forage) comprised a generally increasing proportion of the herd's energy expenditures from April to March (with the exception of December and January, where grazing times were unusually low), with proportions rising from 68% in April to 85% in March. It can be speculated that this shift in activity emphasis improved the net energy balance of the animals, at least during the daylight hours, by largely eliminating those periods of high negative energy flow and increasing periods of positive or neutral energy flow.

The extent to which the herd's activity costs exceeded BMR's appeared consistent with the literature. Moen (1973) found multiples of BMR, calculated from the costs of five different activity regimes of a 60 kg white-tailed deer, to vary from 1.23 to 1.98 x BMR. Similarly, activity costs of a 60 kg pronghorn were equivalent to 1.45 x BMR. Unlike this study, Moen (1973) demonstrated declining multiples of BMR from summer to fall to winter. However, this decline was largely the result of Moen's use of a standard BMR value throughout the year. Consequently, when less "expensive" activities (i.e. bedding, ruminating) began to comprise a larger proportion of the animals' day, the daily activity costs became less expensive, relative to BMR. Had Moen included expected seasonal variations in BMR, a less obvious trend would likely have arisen.

That the peak lactation period of the captive herd was the most expensive time of year, even more so than pregnancy, is consistent with the findings of researchers of animal bioenergetics. Gaines (cited in Blaxter 1962) developed a general formula for the energy content of milk, where kcal/kg in milk = 304.8 + 114.1 f (f = fat content). Since the fat content of milk of a California bighorn ewe during the first 44 days of lactation has been measured at 5% (Atkinson 1980), the caloric value of this milk would be approximately 875 kcal/kg of milk produced. Assuming that sheep are 60% efficient at converting metabolizible energy into milk (estimated efficiency for dairy cattle, from Mollgaard 1929, cited in Blaxter 1962), and that they produce milk at a rate of 1.6 kg/day (minimum value estimated for domestic sheep during peak lactation, from Munro (1962)), milk production for a bighorn ewe would require at least 2300 kcal of energy above that used for maintenance on a daily basis. This would result in an energy expenditure 1.7 times that estimated for May activity costs, a multiple even higher than predicted by Moen (1973) for deer. Pregnancy, even in its final stages, is relatively inexpensive, a fact which has largely been attributed in domestic sheep to the relatively low metabolic rate of the lamb in utero, estimated to be similar per kg of weight to that of the adult ewe (Blaxter 1962). Consequently, ..."in practical trials, it has been difficult to measure any increase in the energy needs of the pregnant animal per kg of her total weight." (Blaxter 1962).

SUMMARY

SOCIAL ORGANIZATION

1) Agonistic interactions between adult ewes were brief, primarily butts or horn threats. It is postulated that the conspicuous absence of horn displays, characteristic of bighorn rams, was the result of limited variability in horn size of the adult ewes.

2) Interactions between ewes were infrequent, relative to that reported for rams. It is postulated that this reduced social activity is a general behavioural strategy adopted by ewes to minimize energy expenditures on activities not vital to maintenance or to reproductive success.

3) A dominance hierarchy developed among adult ewes. However, because of several dominance reversals, the hierarchy was not linear. It was postulated that the homogeneously distributed food resources of the ewes reduced food competition, thus eliminating the need for a rigidly maintained and orderly hierarchy.

4) The hierarchy, although neither rigid nor linear, remained relatively stable over the study period. A rise in status of two relatively low ranking ewes appeared related to their reproductive success.

5) Neither horn lengths nor body weights were shown to be strongly and consistently correlated to social status. Because aging techniques were considered accurate only to six years of age, the relationship between age and dominance could not be adequately investigated. Aggressiveness (i.e. number of interactions initiated) was the only variable found to be significantly and consistently correlated to social status.

CONSEQUENCES OF DOMINANCE

1) Dominant animals did not have higher quality diets than subordinate animals, based on comparison of fecal N and time spent at supplemental feed. It was postulated that dominance during feeding is beneficial to an animal only when both feed and feeding spaces are limited.

2) Dominant animals did not have reduced feeding times or increased bedding times compared to subordinate animals. It was postulated that similar diets resulted in similar activity budgets.

3) Dominant animals were not more productive than subordinate animals, in terms of seasonal weight fluctuations, winter mortality rates or lamb production. It was postulated that similar diets of the social classes resulted in similar levels of productivity.

FORAGE AVAILABILITY AND HERD BEHAVIOUR

1) The herd's diurnal activity pattern was characterized by successive feeding and bedding periods in spring and summer. Activity peaks generally declined in number and increased in duration during fall and winter periods. Although daylength and weather conditions were shown to affect activity patterns to a minor degree, it was postulated that reduced intake rates in the fall and winter resulting from declining forage availability were more directly responsible for the increase in duration of activity bouts during this period of the year.

2) Although daylight grazing times were relatively constant throughout the year, with the exception of December and January values, the proportion of daylight devoted to feeding generally increased from early spring (April) to late winter (March). It was postulated that animals compensated for reduced intake rates during the fall and late winter months by increasing nocturnal grazing periods. The reduced grazing times in December and January coincided with the most inclement weather of the winter and a supplemental food supply, respectively.

EFFECTS OF PHYSIOLOGICAL CONDITION ON DAILY ACTIVITY BUDGETS

1) Prior to their winter deaths, most moribund animals demonstrated increased grazing times relative to healthy animals. Immediately prior to death, moribund animals generally had similar grazing times but increased bedding times relative to healthy animals.

2) The feeding and bedding times of pregnant ewes did not differ significantly from non-pregnant animals.

ENERGY EXPENDITURE ESTIMATES FOR THE HERD

1) Both average BMR's and daylight activity costs for the ewes were higher in spring (April to June) than in summer, fall, and winter.

2) It was demonstrated that, with the exception of December and January values, the proportion of daylight energy devoted to those activities providing gross energetic returns (i.e. feeding, bedding-ruminating) generally increased from spring (April) to late winter (March).

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